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BREEDING STRAWBERRIES (FRAGARIA X ANANASSA DUCH.) FOR ADAPTABILITY TO MACHINE HARVEST AND CYTOGENETICAL STUDIES OF PARENT AND PROGENY

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# Breeding strawberries (*Fragaria* x *ananassa* Duch.) for adaptability to machine harvest and cytogenetical studies of parent and progeny

by

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# INTRODUCTION

Strawberry breeding has received the consideration of horticulturists for the last century to meet the needs of consumers. Each year, many new cultivars appear on the market, but from these only a small number persist, and the majority are discarded.

Changes in labor supply and other economic factors indicated that mechanical harvesting of strawberries is needed to maintain or increase yield without excessive increase in production costs. Hence, for rationalization of strawberry harvest, the construction of picking machines has been initiated. To utilize mechanical adaptation, however, it is necessary to have adapted strawberry cultivars. Cultivars should display high total usable yields, concentration of fruit maturity, firm berries, and good capping quality, which are important clonal traits related to mechanical harvesting adaptability.

The purposes of this study were to evaluate critically the chosen parental clones and their progenies with regard to yielding ability, concentration of fruit maturity, firmness of the fruit and easy cap traits, and, also, to determine the effects of parental matings on these characters as related to mechanical harvesting.

Moreover, the inheritance of these traits attracted the attention of many workers since the early 1900s. Cytological studies, as well, captured the interest of other groups of investigators. Many attempts have been made to investigate the cytological behavior of the chromosomes and the type of chromosome pairing during meiosis. However, a few attempts were made to study the nature of mitosis of octoploid cultivated strawberries.

Other objectives of the present study were to compare the variation in the chromosomal association during meiosis between the progenies and their parental clones, and to investigate the nature of any association between the bivalents during diakinesis and metaphase I. Also, mitosis was investigated in root tip cells of all genotypes studied to determine whether specific chromosomes could be identified.

# PART I.

# BREEDING STRAWBERRIES (*Fragaria* x *ananassa* Duch.) FOR ADAPTABILITY TO MACHINE HARVEST

# INTRODUCTION

The octoploid cultivated strawberry (*Fragaria* x *ananassa* Duch.) is considered a hybrid derived from crosses between *F. virginiana* Duch. x *F. chiloensis* (L.) Duch. (74, 82, 83, 93, 97). Because of their delicate flavor, dessert quality, and nutritional value, strawberries are grown throughout the world and considered one of the very important small fruits crops. It should be available to consumers at low cost. Unfortunately, inflation in recent years, as well as the increasing cost of manual labor for picking strawberries, caused a rapid rise in production costs. The risk for the future is that strawberries could be considered a luxury crop and out of reach of the majority of consumers, unless some modifications in production can receive immediate attention.

One of the most important problems in strawberry programs is how to eliminate increasing production costs year after year. Mechanical harvesting is a possible solution for stabilizing the strawberry industry. In recent years, invention and construction of picking machines in many different locations in the world have been activated. Berries can be stripped from plants by several devices including the use of scoops, tines, air blast or vacuum force, and subsequent use of conveyors (1, 5, 6, 11, 12, 13, 14, 39, 40, 45, 46, 47, 79, 91). Therefore, it is clear now that mechanical harvesting of strawberries is both possible and feasible.

In developing cultivars adapted for machine harvest, the nature of strawberry plants and fruit characteristics should receive due consideration. It is difficult for the breeder to develop a new cultivar in a short period of time; it may take a long time to breed for one or a few traits

needed for machine harvest. It may take a lot of work through the processes of selection, breeding, and identifying the selection that is suitable for that purpose. The nature of strawberry inflorescence is such that fruits at different positions on the inflorescence ripen at different times, resulting in an extended period of fruit maturity (25). Hondelmann (41) stated a special problem could arise by positive correlation between high yielding capacity and length of ripening season.

In breeding strawberry cultivars for once-over harvest, genetic modification in certain fruit and plant characteristics have been suggested (17, 31). Cultivars developed for mechanical harvesting should display concentrated ripening which is defined by Denisen and Buchele (29) as "the tendency of a plant to ripen all or most of its fruit within a short period of time." However, the major problem in many breeding programs is to develop cultivars that can produce high yields of acceptable fruits in a short period of time.

Mechanical harvest-type cultivars should have firm fruits or resilient fruits. Breeding for firmness is of great importance, since soft fruits generally may be more easily damaged than firm fruits during harvesting. Firmness is also of importance for allowing berries to hold better in the field delaying the harvest for more fruit to ripen. Also, good capping quality, the calyx remaining attached to the plant, has been suggested in developing cultivars for machine harvest. As well as good quality, large fruit size, good appearance, upright fruit stems which keep the fruit in a very good position for the machine to harvest were suggested in different breeding programs in order to facilitate once-over or single harvest.

In an attempt to develop certain strawberry selections adapted for machine harvest, this study was conducted in Iowa for more than four years. The objectives of this research were to investigate:

1. The effect of crosses between different selected parental clones on certain characteristics suggested for developing cultivars adapted to machine harvest;
2. Comparative studies between the selected parents and their $F_1$ populations with regard to these characteristics.

# LITERATURE REVIEW

The shortage of pickers at harvest time, as well as the dislike of manual labor for picking strawberry fruits, represent a very serious problem that faces the production system in the United States and other areas in the world. From this point, numerous workers have been involved in many different breeding programs for developing different strawberry clones adapted to once-over harvest (8, 10, 16, 22, 27, 30, 31, 37, 38, 42, 62, 73, 78, 91). Thus, adaptability to mechanical harvesting became the most important objective for many breeding programs (2, 4, 15, 30, 43, 50, 51, 78, 89, 90). Denisen at Iowa State University was probably the first one to direct attention toward both breeding for new cultivars and evaluating the existing clones with characteristics adapted to once-over mechanical harvesting.

Breeding for concentrated ripening, the ability of a plant to ripen all or most of its fruit within a short period of time, is considered as the most important trait. Other breeding programs with the same objective have been initiated at many different experiment stations and institutes including Arkansas, California, Florida, Illinois, Michigan, and Oregon. They developed different types of harvestors designed for once-over harvest. In addition to concentrated ripening of fruit, other characteristics, such as firmness, easy capping or easy break pedicels, have been suggested (31). In recent years, certain cultivars displaying various degrees of concentrated ripening of the fruit have been evaluated (3, 25, 30, 56). The type of inheritance of plant and fruit characteristics of strawberry cultivars as related to machine harvest captures the attention of

another group of workers (9, 18, 19, 22, 24, 31, 51, 70, 76, 77, 81, 82, 84, 85, 86, 96).

In his report, Davis (26), indicated that strawberry production increased by 87% in the 20-year period ending in 1967. This is a greater percentage increase than for other fruit or nut crops. Other statistical data indicate trends which further emphasize the need for mechanization in strawberry harvesting. High labor costs as well as inadequate number of pickers at the picking time caused rapid increases in the costs of strawberry production. In comparison between the production costs of the strawberry with other costs, Denisen and Buchele (30) indicated that hand harvesting may account for 1/3 to 3/4 of the total. In another study, Morris (67) stated that hand harvesting is no longer feasible or available for most processing fruit crops. In small fruits crops such as blackberries and strawberries, hand harvesting costs account for 1/2 to 3/4 of the total cost. He concluded that, unless mechanical harvesting replaces hand picking for these crops, their processed products could be relegated to luxury foods outside the reach of the majority of consumers. In the most recent report, Rosati (80) stated that, because of inflation in recent years, the cost of producing strawberries has increased continuously at a rate of about 22 percent per year. Consequently, methods to reduce production costs are urgently needed, or there will be a shortage of strawberry acreage and production in the near future.

The expectation is that mechanical harvesting will reduce the labor costs; however, the study of Buchele and Denisen (21), who economically analyzed the mechanical harvesting costs, indicated there may not be much monetary saving by using a machine instead of hand labor, since the

machine will not be able to distinguisn between green and mature fruits; also, damage will result from a once-over harvest. Therefore, reduction in total yield will be expected. A hypothetical case study estimated a yield loss of about 25% due to machine handling. The loss was anticipated as due to losing berries either through damage from bruising or spoilage of the overripe berries. Also, some of the berries may not have fully developed and were not adequately mature for harvest (21).

A very good definition has been applied to the term of mechanical harvesting by Booster (11), who defined it as,

> ... the harvesting of a crop through the use of power equipment. By some mean or others the mechanical device removes from the plant the part or parts desired, places the detached material into a suitable container for further processing, and rejects the unwanted portion of the plant.

Because of the wide variation among cultivars, such as the growth habit and fruit characteristics which may influence external as well as internal factors, he emphasized that those characters complicate the use of machines; therefore, applying this definition to the harvesting of strawberries is a real challenge.

For utilizing mechanical harvesting, it is necessary to have the right kind of strawberry cultivars. The selected clones should be concentrated-ripening types with all or most of the berries on a plant ripe at one time. Other requisites include a brittle peduncle, easy cap tendencies, and the quality factors of good flavor, good holding, and relative resistance to bruising. The variety must also be a good yielder, particularly considering some yield will be sacrificed to handle the crop mechanically (28, 29, 30, 31, 32, 33, 35, 36, 41, 52, 53, 55, 56, 60, 61, 63, 67, 69, 86, 89).

Thus, genetic modifications of plant and fruit traits through breeding programs become essential for developing new clones adapted for once-over harvest. Bringhurst (17) reported that type of fruit must be amenable to first, mechanical calyx removal, and second, mechanical removal from the plant. The available genetic stocks have been scrutinized for the necessary traits and significant progress in breeding completed. It should be possible to develop optimum formed fruit and plants as rapidly as suitable mechanical devices are invented and developed.

The removal of the strawberry fruits from the plant is either the calyx and stem still attached to the plant (easy-cap -- this step is required for processing) or the calyx and stem attached to the fruit (easy break pedicel). In one direction, breeding programs for developing cultivars that show either or both characteristics have been initiated in many places. In the other direction, a search was made for the invention of capping and stemming devices that facilitate the mechanical harvesting satisfactorily (48, 49, 57, 59, 64, 65, 66, 92, 94). With regard to easy calyx removal trait, Barritt (9) reported that parent clones showed a wide variation for this character. He found that general combining ability values vary from one parent to another, and the values were closely associated with parent phenotypes. The conclusion is that a high proportion of genetic variance of capping ease is additive; therefore, selecting parents on the basis of their phenotypes would produce predictable genetic gain in offspring performance.

The evaluation of the genetic sources of fruit detachment character in strawberry by Brown and Moore (18) indicated that capping force did not differ significantly among cultivars nor species. Although the clones did

not differ phenotypically in requiring capping force, progenies from *F. ananassa* x *F. virginiana* crosses required significantly less force to cap than progenies derived wholly from *F. ananassa*. No clear relationship exists between capping percentage and pedicel breaking force; apparently they are under different genetic control. The data of their work suggested that a proper combination of low capping force and high pedicel breaking force can be found in recombinations involving crosses within the cultivated strawberry.

Another study by the same authors (19) provides evidence that capping percentage, capping force and pedicel breaking force were all significantly correlated with each other and were highly influenced by environment, and had relatively low heritabilities. They concluded that parent phenotypes could not be used to predict progeny performance, but the general combining ability scores were useful for identifying promising parents. Combination of additive genes and dominant genes controlled the capping force trait.

By using the capometer for determining the force required to detach the strawberry fruit from the plant, Brown and Moore (20) found that capping percentage obtained by hand, as well as that obtained by the capometer device, force required to break the pedicel, and force required for capping were significantly correlated with each other. They summarized that measurements as obtained by the capometer will facilitate the development of cultivars with the potential for capping and with the pedicel strength desired for mechanical harvest.

Emphasizing the traits required for mechanical harvesting of strawberries, Denisen and Buchele (29) pointed out that certain concepts

involved in the mechanical harvesting of strawberries requisite to shift from manual production to mechanical harvesting methods. These are: a) harvesting must be accomplished without excessive costs, b) it may be necessary to sacrifice some of the crop to do the operation by machine, c) a one-crop harvest is assumed; consequently, there is need for varieties with concentrated ripening, which only recently has become a breeding objective, d) since strawberries are used both on the fresh market and for processing, it is assumed that machines will meet the needs of both uses, e) characteristics of berries for machine harvest require brittle peduncles and easy capping tendencies or both, and f) the berries need not be large. With machine harvest, there will be a trend toward smaller berries because large berries generally bruise easier than small berries. Mechanical harvesting of strawberries is urgently needed to stabilize the industry.

Strawberry harvest mechanization presents an even greater challenge than for most other horticultural crops (30). In this paper, Denisen et al. reported that, since strawberry fruits are produced very close to the ground, they are easily bruised when handled by machines, and they have in the past, at least, required a multiple harvest. The conclusion is that machine harvesting appears as the potentially best answer for harvesting strawberries because of increasing dislike for the manual labor of picking strawberries.

Again, Denisen et al. (32) concentrated their attention on the concentrated ripening trait, in addition to certain other features considered essential for adaptability to machine harvesting, such as easy cap, easy break pedicel, high yielding ability, firmness of the fruit, and relative resistance to bruising. They postulated that ease of capping becomes an

important criterion for evaluation of seedlings of cultivars when selecting for machine adaptability. Some cultivars are better adapted than others to mechanical harvest because a higher percentage of berries mature at one time. Because the machine could not distinguish between green and ripe berries, great emphasis was placed on the concentrated ripening character. Variability among cultivars with regard to these characteristics that were required to facilitate the mechanical harvesting of strawberries presents possibilities to produce new adapted cultivars through breeding and selection (28).

In 1971, Garren wrote that, if strawberries are to be harvested mechanically, it is going to require the close cooperative effort of a number of people. The engineer-inventor will do all that he is able within the limits of his skills. The plant breeder-geneticist will do his best to modify and develop plants most adapted to the particular mechanism used to effect the harvest. The general aims of the breeding program are to develop plants that produce fruit of uniform size, shape, and color that mature or ripen at the same time and are readily separated from the parent plant (33). Such plants should not encumber the machine with stems, runners, and leaves. The fruit should be firm, cap and stem separation should occur cleanly and easily, and the quality and yield of fruit should be high.

In another report, Garren (34) stated that the invention of the machine devices, breeding for more adaptable cultivars, cultural adaptation, and new development in handling the crop in processing plants are harbingers of mechanical harvesting.

Considerable attention has been given by many workers for the high yielding capacity of the cultivars adapted for mechanical harvest. Gooding (35) reported that cultivars for machine harvest should display increasing yields to offset losses caused by once-over harvesting. Also, firmness and bruise-resistance were necessary for developing cultivars suitable to machine harvesting. In the same subject, Guttridge and Anderson (36) considered that concentrated ripening is an important character. They found the higher-yielding cultivars had the more concentrated ripening periods as measured by percentages of marketable fruit harvested at a single picking. Hondelmann (41) reported that cultivars adapted for mechanical harvesting are to display a concentrated ripening period, upright fruitstems, which keep the fruit in this position, very firm and large berries, and an extremely good capping quality or to break off their peduncles very easily. He hypothesized that extremely good capping quality can be reached by use of decaploid strawberry genotypes in breeding programs. He also pointed out that firmness of fruit is the very important characteristic which is built up by two components: toughness of skin and firmness of flesh, which were correlated to a certain extent. Both components show a considerable degree of variability. He considered the ability of the cultivar for high yield a very important character, but a special problem could arise if there is a positive correlation between high yielding capacity and the length of ripening season.

Lawrence (52) stated that adaptability for machine harvest requires cultivars with concentrated ripening of the crop and a ready separation of the fruit from the plant with or without caps. He also reported that the concentrated ripening character is greatly influenced by weather. He

added that firmness of fruit is considered another important trait for cultivars developed for machine harvest.

By using a capping ease rating system, Lawrence et al. (55) found that crossing in which both parents were easy cappers produced a higher proportion of easy capping seedlings than when only one parent was an easy capper. Negative correlations were found between the percentage of easy cap types and fruit firmness. The highest percentages of easy cap types had soft fruit. Also, negative relationships between yield and fruit size were found in some clones.

For developing new processing strawberry cultivars for machine harvest, Lawrence (53) defined the primary traits needed for that purpose as concentrated ripening of the crop, fruit accessibility for complete removal of the crop, a very firm berry with a resilient (tough) skin, good processing quality, ease of capping, and high yields. He determined that 90% to 95% ripe fruit is important to mechanical harvesting because this will provide the processor with as little as 5% cull fruit from a ripeness standpoint. He also reported an upright fruiting habit is considered a necessary character for machine harvest, but it may be related to fewer fruits per truss and smaller berries – two characters detrimental to yield. Obtaining easy capping berries that are firm and have good processing qualities has been a serious problem. Finally, he concluded "... it is essential to have cultivars and clones that produce a high percentage of the total crop as ripe fruit for a once-over harvest." Lawrence and Martin (54) reported that easy cap is considered as one of the most important traits in selection for machine harvest; that can be transmitted from some parents

to their offspring through crossing. Also, usable fruit yields cannot be obtained without a high percentage of fruit ripe at one time. Concentrated ripening increases efficiency through less waste, and better product utilization provides advantages important to the processor.

In evaluation of some strawberry cultivars and selections, Moore and Brown (60) pointed out that there is no clone that produces over 40% acceptable fruit at any single harvest. Total yield is an important trait for evaluating the once-over harvest potential, since the amount of usable fruit that can be harvested at any one time is determined by the percentage of fruit ripe and the total productivity of the cultivars. Environmental effects on the concentrated ripening character were noted during this study; the warm season during harvesting hastened berry ripening and concentrated the maturity, while the cool, wet, cloudy conditions extended the fruit maturity period. They concluded that concentrated ripening in strawberries appears to be amenable to genetic improvement. The actual usable yield at a given time is the product of the percent of the fruit that is ripe and the total amount of fruit on the plant. The combination of high seasonal yield and high percent concentration of ripening would result in the greatest single harvest yield (63). Breeding strawberries for adaptation to mechanized harvest presents some unique and difficult barriers (61); the fruit of the strawberry is very delicate and requires gentle handling. Furthermore, the fruit is borne near the ground, making retrieval by machine difficult and limiting the systems available for fruit removal. Perhaps the greatest obstacle, however, is the nature of the fruiting habit of the strawberry. Fruits borne at different positions on the cymose inflorescence ripen at different times, resulting in an extended

period of fruit maturation. They summarized that concentrated ripening, high productivity, easy fruit detachment, and fruit firmness are the important characters that relate to mechanical harvest. Also, Morris et al. (68, 69) came to the same conclusion.

In evaluating the response of certain strawberry clones to hand picking prior to once-over machine harvest, Morris et al. (69) found that some clones were not suited to machine harvest, with or without hand picking before the once-over operation. Clones that have high yields and do not concentrate fruit ripening can be hand picked once without a significant reduction in machine-harvest yield. In a once-over harvest operation, the early ripening primary fruits of some clones are sacrificed to decay to allow the majority of the crop to ripen. However, hand picking before once-over machine harvest was not necessary for some clones, because of their concentrated fruit-ripening pattern and superior firmness and field-holding ability.

The work of Nelson and Kattan (71) indicated that three basic functions must be performed by the harvester, i.e., the fruit must be stripped from the plant, separated from the leaves and other foreign material, and conveyed to transport containers. Because of the nature of the strawberries that the mature fruit is borne near the ground, they emphasized that a picking device is required to lift the fruit from the ground without disturbing the soil surface or damaging the berries.

Once-over mechanical harvesting is feasible even with existing strawberry cultivars. Genetic, cultural, and physiological approaches which may concentrate fruit set at a higher single plane position on the plant would automatically increase the percentage of acceptable yields (31, 72,

88). Nelson and Morris (72) assumed that some change will be required in the handling operation to accommodate the mechanically harvested fruit. There will be increased sorting and grading requirements resulting from the presence of both green and overripe fruit. Most of the fruit will have the calyx and part of the pedicel attached, and these must be removed before the berries can be processed.

In studying certain fruit characteristics of some seedlings of *F. virginiana* crossed with cultivated strawberry cultivars, Scott (81, 82) reported that large size of fruit is one of the most important economic characters sought in breeding commercial cultivars of strawberries. He found that small fruit size of *F. virginiana* and *F. chiloensis* is partially dominant to the large fruit size in modern cultivated cultivars; and large fruit size can be recovered quickly by backcrossing and outcrossing to large-fruited types. He concluded that fruit weight characteristic may be governed by a number of genes; and no significant correlation between fruit size and firmness of fruit. But a negative correlation between fruit size and number of berries per plant was found; for the $F_1$-average, the number of fruits per plant was large as in parent-average, but $F_1$ plants had smaller fruit-size than the parent-average (77). By the same token, Baker (7) found the hybrids of strawberry resulting from crosses between inbred populations were significantly larger in fruit size than any of selfed population. Heterosis for fruit size of some progenies resulted from crosses between cultivated types. He concluded that size of fruit is inherited quantitatively, with several genes involved.

As mentioned before, the importance of firmness of fruit as related to mechanical harvesting is due to two reasons: 1) firm fruit can resist

damage that may be caused during machine operation, 2) firm fruit can be held better for a long period of time allowing more fruits to ripen. Many instruments have been constructed in order to measure fruit texture and firmness for evaluating the cultivars and identifying which are suitable for mechanical harvesting (23, 44, 75, 95). In using the instron machine to measure skin toughness and flesh firmness, Ourecky and Bourne (75) identified several selections that had tough skin such as 'Tennessee Shipper', which is considered the most firm.

Sistrunk and Moore (86) reported that firmness and color of ripe fruit are perhaps the major quality attributes of cultivars mechanically harvested for processing. Internal and external structure of strawberries greatly influences the textural properties and resistance to breakage and disintegration during harvesting and handling. There is a wide range in these properties among different genotypes that must be recognized and defined early in a breeding program. Also, a wide range in firmness for cultivars at different ripeness levels was evident.

Regarding breeding for concentrated ripening, Denisen et al. (31) stated that this characteristic has been shown to be transmitted from one generation to the next by genetic principles. It is also well-known that easy-cap tendency is inherited. With regard to the effect of the external factors, Denisen et al. (32) pointed out that concentrated ripening types do not follow the traditional primary, secondary, tertiary, etc. sequence in ripening, but tend to "bunch" them together. This phenomenon usually occurs as a result of aborted blossoms. In some instances, the primary berry does not develop, the secondary and tertiary berries develop almost simultaneously, and the quartenary and quintary blossoms tend to abort.

They also reported that parents with concentrated ripening have produced several seedling lines that are even more concentrated in ripening than the parents. In addition to that, plant population or spacing has considerable influence on concentration of ripening, i.e., when plants are crowded, the berries are more inclined to ripen simultaneously or nearly so than when each plant has abundant space. It is under crowded conditions that most abortion of late blossoms occurs if a cultivar is inclined to concentrate its production. They generalized the case as perhaps competition for light and nutrients may be an important factor which tends to concentrate ripening. Also, Stang (88) found that plants of the same clone produced less concentrated ripening if grown in the greenhouse than when grown with more competition in a bed out-of-doors.

As seen through the brief historical story of the strawberry mechanization, breeding for characteristics related to once-over machine harvest is a very important target for stabilizing the strawberry industry. There is little doubt that these traits have different patterns in their inheritance and their transmission through the generations, and are under gene control. Like internal factors, external factors should have the same consideration. Many of these characters were affected by the external factors such as temperature, relative humidity, the condensing of the plant population, etc., especially the concentrated-ripening (60).

# MATERIALS AND METHODS

This research was conducted during the 1978, 1979, 1980, and 1981 growing seasons at the Iowa State Horticulture Research Station, northeast of Ames, Iowa.

## Materials

Twenty-six selections of the cultivated octoploid strawberry (*Fragaria* x *ananassa* Duch.) and their respective progenies were used as experimental materials. The twenty-six parental clones have been selected on the basis of their performance with regard to certain characteristics suggested to facilitate the mechanical harvesting of strawberries. The selections were subjected to the crossing procedures.

## Methods

### Crossing procedures

Five plants representing each parent were potted, in 10 cm pots, during the spring and the fall of 1978. The potted plants were transferred to the greenhouse and were more conveniently located to each other so the progress of the flower and the fruit development could be more closely observed. These plants received all the cultural practices of the greenhouse operation.

Flower buds were emasculated as soon as the white corolla became visible. By using a pair of straight forceps, the anthers were removed together with the perianth with a minimum of injury to the receptacle. All open flowers and all buds except those to be used were removed before emasculation and the plant was subjected to a thorough spraying under a stream

of water to remove any pollen which may have adhered to the leaves; the latter step was as described by Mangelsdorf and East (58).

The crosses were made randomly between the different twenty-six parental clones, so that one parental clone was generally involved in more than one cross. The source of pollen was a parent plant that had some opening flowers with mature anthers. Immediately after emasculation, pollen grains from the male parent were transferred to the stigmas of the female parent. Satisfactory cross pollinations were made, using a fine camel's hair brush. After pollination, ample protection was made by removing the pollinated female plants to another place to avoid contamination with pollen from other *Fragaria* plants. Each pollinated plant was labeled with the parentage of the cross.

Later on, at the time of fruit maturity, the berries of each hybrid were collected in a separate bag; the outer thin layer of the berry which contains the seeds was carefully removed using a very sharp knife. These thin layers were planted in plastic Jiffy trays (31 cm x 10 cm) which contained a mixture of 1 soil:1 peat:1 perlite. Upon seedling emergence (about 5-6 weeks from planting), good care was taken with regard to all cultural practices such as watering, weed control, spraying, fertilizing, etc.

When the seedlings reached about 3 cm high, they were transplanted into 57 $mm^2$ Jiffy peat pots containing the same greenhouse soil. After two more months, when the seedlings reached about 10 cm high, they were prepared for transplanting outdoors in field plots.

All the progenies which had less than ten individual seedlings were excluded. Those progenies that resulted from crosses between the plants potted during the spring of 1978 were transplanted outdoors in the fall of

the same year, while those that resulted from crosses between plants potted during the fall of 1978 were transplanted in the spring of the following year. The number of progenies resulting from these crosses was eighteen, and they were the same for both 1978 and 1979 transplanting.

Completely randomized design with two replications have been used in this study. Replication number one was assigned for all the eighteen progenies and their twenty-six parents which were transplanted during the fall of 1978. Those progenies and their parents that were transplanted in the spring of 1979 were assigned to replication number two. For both replications, each entity, either progeny or parental clone, was represented by five individual plants which were set at random in each replication in spacing of 120 cm between the rows and 60 cm within the row.

The genotypes used in the present study are as follows:

I. Parental clones

| | | |
|---|---|---|
| 6-75060 | 17-75018 | 22-6963 |
| 25-6943 | 16-75081 | 46-6943 |
| 1-75004 | 24-75003 | 8-75065 |
| 13-75060 | 16-75056 | 42-6943 |
| 20-6971 | 19-6936 | 21-6937 |
| 3-75077 | 19-6935 | 9-6957 |
| 11-75081 | 3-6969 | 6-75123 |
| 1-75092 | 9-7410 | 80-6935 |
| 31-75088 | 14-6967 | |

II. Progenies

| | |
|---|---|
| 7801 (80-6935 x 6-75123) | 7870 (13-75060 x 20-6971) |
| 7810 (8-75065 x 42-6943) | 7873 (19-6935 x 3-6969) |
| 7815 (6-75060 x 25-6943) | 7878 (16-75056 x 19-6936) |
| 7836 (1-75004 x 25-6943) | 7882 (22-6963 x 9-6957) |
| 7846 (21-6937 x 19-6935) | 7886 (3-6969 x 22-6963) |
| 7854 (14-6967 x 25-6943) | 7889 (16-75081 x 24-75003) |
| 7856 (46-6943 x 3-6969) | 7890 (3-75077 x 11-75081) |
| 7858 (9-6957 x 6-75123) | 7899 (17-75018 x 1-75092) |
| 7864 (9-7410 x 19-6935) | 78100 (1-75092 x 31-75088) |

Evaluation of the progenies and their parental clones

During the summers of 1980 and 1981, data were taken to evaluate and to compare the $F_1$s and their parents with regard to yield, concentrated ripening, easy cap (force required for berry detachment), and firmness, and to investigate the possible relationships between these traits.

To evaluate these entities for their performance, four harvests with three-day intervals were used. For determining the total yield, the number of mature berries for each plant were collected and recorded at each harvest; at the end of harvesting, the sum of the number of berries for the four harvests represented the total yield per plant.

The concentrated ripening character for each plant was determined as the percent of mature berries at each harvest as related to the final total yield.

The easy cap trait was determined using a Chatillon Fruit and Vegetable Tester with a 1000 g capacity, in 10 g units, that was modified to

measure the force required to detach the strawberry fruit from the calyx. A holder made to the specifications provided by Brown and Moore (20) was secured to the hook on the pressure tester by a clamp. The holder was a wire attached to a diam steel washer, which was milled to hold a polyethylene funnel. The funnel's narrowest portion was removed, making a uniform cone. The only deviation from Brown and Moore's model was that, instead of making a slit in one side of the funnel cone to facilitate the insertion of the fruit and pedicel, four different sizes of cones were developed to fit any berry size. After the modification, the dimensions of the funnel cones were as follows: the funnel's largest diameter was 63 mm, and the smallest was 32 mm. The length of the side was 29 mm. The dimensions of the other three cones were 63 mm, 27 mm, and 37 mm; 35 mm, 15 mm, and 17 mm; and 25 mm, 8 mm, and 17 mm, respectively (Appendix).

Three fruits chosen at random from each of the five plants that represented each entity in a separate bag at each harvest were selected for determining the force required for separation of the fruit from the calyx. Fruit was detached from the plants, with calyx and pedicel attached, by pinching through the primary pedicel just above the points of attachment for the secondary pedicel. Each fruit was placed in the holder and the pedicel pulled straight down, directly away from the apex of the fruit, as described by Brown and Moore (20) (Appendix). The force at which the fruit was capped was automatically indicated by a pointer which stayed at the maximum reading. The average of the three measurements was recorded for each plant at each harvest.

Fruit firmness was measured by using a Chatillon Fruit and Vegetable Tester (Model 516-1000 MRPFER) with a 1000 g capacity, in 10 g units. Modification was made by placing a small steel portion with diameter equal to 8 mm at the top of the apparatus (Appendix). Three fruits were used for determining the firmness by placing the fruit over the steel portion and pushing down by fingers till the penetration of the steel portion was equal to 5 mm in the berry flesh (Appendix). The measurement was indicated by a pointer which stayed at the maximum reading. The average of the three measurements was recorded for each plant at each harvest.

## Statistical analysis

Data of 1980 and 1981 growing seasons were statistically analyzed according to Snedecor and Cochran (87) as follows.

Completely randomized model This model was used for determining the variations among the progenies, among the parents, and between the progenies and their parental clones, for each attribute as follows:

$$Y_{ij} = R_i + S_j + \varepsilon_{ij}$$

where

$R_i$ = replication effect;

$S_j$ = entity effect.

The above model was fit to give the typical ANOVA:

| Source | d.f. | S.S. | M.S. | F |
|---|---|---|---|---|
| Rep | 1 | | | |
| Entity | 43 | | | |
| Among progenies | (17) | | | ← $F_1$ |
| Among parents | (25) | | | ← $F_2$ |
| Progenies vs. parents | ( 1) | | | ← $F_3$ |
| Error | 43 | | | |

where

$F_1$ gives a test for differences among progenies;

$F_2$ gives a test for differences among parents;

$F_3$ gives a test for differences between parents and progenies.

A closer examination of how progenies compared to their parental clones was investigated by the following partitioning to the sum of squares.

| Source | d.f. |
|---|---|
| Rep | 1 |
| Entity | 43 |
| Progenies vs. own parent | 1 |
| Remainder | 42 |
| Error | 43 |

This is just another way of looking at the previous ANOVA. To answer the question of specific comparisons of progenies to their own parents, multiple t-tests were performed.

Split plot design For determining the changes of the traits through the 4 harvesting periods, split plot design was used. For each attribute, the model

$$Y_{ijk} = R_i + S_j + \underbrace{(RS)_{ij}}_{\text{Error a}} + H_k + (SH)_{jk} + \underbrace{(RH)_{ik} + (RSH)_{ijk}}_{\text{Error b}}$$

where

$R_i$ = replication effect

$S_j$ = entity effect

$(RS)_{ij}$ = replication * entity interaction

$H_k$ = harvest effect

$(SH)_{jk}$ = entity * harvest interaction

$(RH)_{ik}$ = replication * harvest interaction

$(RSH)_{ijk}$ = replication * harvest * entity interaction

was fit to give the typical ANOVA as follows:

| | Source | d.f. | S.S. | M.S. | F |
|---|---|---|---|---|---|
| | Rep | 1 | | | |
| | Entity | 43 | | | $F_1$ |
| $E_a$ | Rep * entity | 43 | | | |
| | Harvest | 3 | | | $F_2$ |
| | Entity * harvest | 129 | | | $F_3$ |
| $E_b$ | Rep * harvest | 3 | | | |
| | Rep * entity * harvest | 129 | | | |

where:

$F_1$ gives a test for differences among entities;

$F_2$ gives a test for differences between harvest dates;

$F_3$ gives a test for entity * harvest interaction.

Since the harvest dates appeared to be different, it was natural to investigate the nature of this difference. This is analyzed by looking at the type of entity * harvest interaction. If this interaction is not significant, an ordered ranking of harvest means gives an indication as to which harvests are superior. If there is an interaction existing, Tukey SS can be pulled out from the interaction SS, and if this subdivision turns out to be significant, then the ordered ranking is still useful.

Regression models

I) $Y_i = \beta_0 + \beta_1 H_i + \beta_2 H_i^2 + U_i$

where

$Y_i$ = yield mean of $i^{th}$ harvest;

$H_i$ = harvest period; $H_i$ is 1, 2, 3 or 4.

$U_i$ = error term.

II) $F_i = \beta_0 + \beta_1 C_i + U_i$

where

$F_i$ = firmness mean of $i^{th}$ entity;

$C_i$ = capping force mean of $i^{th}$ entity;

$U_i$ = error term.

III) $Y_{ij} = \beta_0 + \beta_1 E_{ij} + \beta_2 E_{ij}^2 + \epsilon_{ij}$

where

$Y_{ij}$ = yield mean of $j^{th}$ entity during $i^{th}$ harvest;

$E_{ij}$ = concentrated ripening mean of $j^{th}$ entity during $i^{th}$ harvest.

Correlation Correlation coefficients between yield and concentrated ripening, and also between firmness and capping force, were computed to give an indication of what might be strong linear tendencies. Where such an indication appeared, further investigation into the nature of these tendencies was made.

# RESULTS

## Evaluation of the Progenies and Their Parental Clones with Regard to Yield (Number of Berries per Plant), Firmness (gms.), and Capping Force (gms.)

### Yield (number of berries per plant)

The data on the average number of berries per plant for the progenies and their parental clones are given in Tables 1 and 2 for 1980 and 1981. The average number of berries per plant in 1980 ranged from 27.30 to 59.80, and from 23.00 to 59.80 for the progenies and their parental clones respectively. In 1981, this average ranged from 27.20 to 59.70 for the progenies and from 24.00 to 60.30 for their parents. F-test with P=.001 was used to detect the differences among the progenies, among the parental clones, and between the progenies and their parents. Tremendous variations for the average number of berries per plant were found within the progenies, within the parents, and also between the progenies and their parental clones in general. Presumably, part of the variation is due to sampling error, although differences between the genotypes were highly significant statistically, especially the variations between the progenies and their parents.

Conservative multiple t-test was used to detect the differences between each specific progeny and its own parents. The results obtained in this study indicated that most of the progenies showed highly significant differences and were superior to their own parents for average number of berries per plant. The difference between the progeny's mean and the average means of its two parents together reflects either the superiority or

Table 1. Means of yield (number of berries per plant), firmness of berry (gms), and force required for berry detachment (gms) of the progenies and their parental clones in 1980[z]

| Genotypes | | Traits or characters | | |
|---|---|---|---|---|
| Progenies | Parents[y] | Yield (no. of berries/plant) | Firmness (gms) | Capping force (gms) |
| 7801 | | 33.30 | 371.03 | 460.78 |
| | 80-6935 | 30.40 | 551.03 | 642.23 |
| | 6-75123 | 34.00 | 384.73 | 491.38 |
| 7810 | | 35.40 | 577.35 | 723.70 |
| | 8-75065 | 44.20 | 450.38 | 587.53 |
| | 42-6943 | 50.20 | 427.40 | 548.33 |
| 7815 | | 29.80 | 707.15 | 772.35 |
| | 6-75060 | 26.20 | 553.53 | 670.75 |
| | 25-6943 | 30.50 | 462.90 | 635.93 |
| 7836 | | 27.30 | 657.58 | 703.33 |
| | 1-75004 | 30.90 | 408.73 | 617.95 |
| | 25-6943 | 30.50 | 462.90 | 635.93 |
| 7846 | | 59.80 | 638.88 | 757.53 |
| | 21-6937 | 59.80 | 518.10 | 628.13 |
| | 19-6935 | 33.10 | 433.73 | 457.13 |
| 7854 | | 43.60 | 581.30 | 770.13 |
| | 14-6967 | 29.90 | 494.85 | 638.35 |
| | 25-6943 | 30.50 | 462.90 | 635.93 |
| 7856 | | 34.00 | 489.33 | 588.38 |
| | 46-6943 | 31.20 | 419.50 | 533.98 |
| | 3-6969 | 29.50 | 452.80 | 580.23 |
| 7858 | | 45.10 | 340.78 | 425.58 |
| | 9-6957 | 30.10 | 490.90 | 531.48 |
| | 6-75123 | 34.00 | 384.73 | 491.38 |

[z]Each figure represents the average of the two replications.

[y]Upper is female parent; lower is male parent.

Table 1. *Continued*

| Genotypes Progenies | Parents[y] | Traits or characters | | |
|---|---|---|---|---|
| | | Yield (no. of berries/plant) | Firmness (gms) | Capping force (gms) |
| 7864 | | 28.70 | 212.85 | 393.20 |
| | 9-7410 | 27.60 | 519.48 | 571.28 |
| | 19-6935 | 33.10 | 433.73 | 457.13 |
| 7870 | | 31.10 | 514.78 | 671.85 |
| | 13-75060 | 27.00 | 480.45 | 600.58 |
| | 20-6971 | 25.10 | 444.13 | 646.25 |
| 7873 | | 49.10 | 585.23 | 662.60 |
| | 19-6935 | 33.10 | 433.73 | 457.13 |
| | 3-6969 | 29.50 | 452.80 | 580.23 |
| 7878 | | 35.70 | 626.00 | 695.65 |
| | 16-75056 | 34.10 | 509.15 | 657.25 |
| | 19-6936 | 40.70 | 571.83 | 673.83 |
| 7882 | | 54.60 | 544.20 | 649.98 |
| | 22-6963 | 34.00 | 549.78 | 585.63 |
| | 9-6957 | 30.10 | 490.90 | 531.48 |
| 7886 | | 27.30 | 341.65 | 413.43 |
| | 3-6969 | 29.50 | 452.80 | 580.23 |
| | 22-6963 | 34.00 | 549.78 | 585.63 |
| 7889 | | 33.60 | 566.48 | 674.38 |
| | 16-75081 | 29.90 | 440.15 | 537.43 |
| | 24-75003 | 27.30 | 502.23 | 613.10 |
| 7890 | | 51.00 | 62[illegible].78 | 736.18 |
| | 3-75077 | 38.30 | 542.70 | 65[illegible].20 |
| | 11-75081 | 35.70 | 550.48 | 649.25 |
| 7899 | | 32.70 | 223.30 | 387.70 |
| | 17-75018 | 24.60 | 374.60 | 667.00 |
| | 1-75092 | 23.00 | 365.60 | 630.30 |
| 78100 | | 34.10 | 436.53 | 675.25 |
| | 1-75092 | 23.00 | 365.60 | 630.30 |
| | 31-75088 | 31.40 | 363.35 | 593.85 |

Table 2. Means of yield (number of berries per plant), firmness of berry (gms), and force required for berry detachment (gms) of the progenies and their parental clones in 1981[z]

| Genotypes Progenies | Parents[y] | Traits or characters | | |
|---|---|---|---|---|
| | | Yield (no. of berries/plant) | Firmness (gms) | Capping force (gms) |
| 7801 | | 34.00 | 366.38 | 462.38 |
| | 80-6935 | 29.90 | 553.15 | 646.65 |
| | 6-75123 | 33.20 | 381.85 | 486.10 |
| 7810 | | 35.70 | 587.70 | 725.93 |
| | 8-75065 | 43.40 | 452.53 | 588.65 |
| | 42-6943 | 50.00 | 428.73 | 545.38 |
| 7815 | | 29.20 | 709.08 | 772.90 |
| | 6-75060 | 26.50 | 551.60 | 672.60 |
| | 25-6943 | 31.20 | 460.10 | 637.85 |
| 7836 | | 27.20 | 685.73 | 707.30 |
| | 1-75004 | 31.50 | 409.20 | 613.23 |
| | 25-6943 | 26.50 | 551.60 | 672.60 |
| 7846 | | 59.70 | 638.98 | 760.68 |
| | 21-6937 | 60.30 | 519.35 | 618.33 |
| | 19-6935 | 32.60 | 432.75 | 451.83 |
| 7854 | | 43.40 | 575.70 | 763.20 |
| | 14-6967 | 29.90 | 491.18 | 624.03 |
| | 25-6943 | 26.50 | 551.60 | 672.60 |
| 7856 | | 33.80 | 485.30 | 582.20 |
| | 46-6943 | 31.10 | 418.46 | 533.08 |
| | 3-6969 | 29.80 | 452.23 | 577.60 |
| 7858 | | 44.88 | 348.89 | 437.40 |
| | 9-6957 | 31.30 | 488.78 | 531.35 |
| | 6-75123 | 32.20 | 381.85 | 486.10 |

[z]Each figure represents the average of the two replications.

[y]Upper is female parent; lower is male parent.

Table 2. *Continued*

| Genotypes Progenies | Parents[y] | Traits or characters | | |
|---|---|---|---|---|
| | | Yield (no. of berries/plant) | Firmness (gms) | Capping force (gms) |
| 7864 | | 27.80 | 213.65 | 394.55 |
| | 9-7410 | 28.10 | 523.70 | 570.78 |
| | 19-6935 | 32.60 | 432.75 | 451.83 |
| 7870 | | 31.00 | 513.13 | 665.60 |
| | 13-75060 | 26.40 | 476.15 | 592.13 |
| | 20-6971 | 26.30 | 442.03 | 646.33 |
| 7873 | | 48.20 | 585.65 | 662.40 |
| | 19-6935 | 32.60 | 432.75 | 451.83 |
| | 3-6969 | 29.80 | 452.23 | 577.60 |
| 7878 | | 35.80 | 630.18 | 702.25 |
| | 16-75056 | 33.80 | 510.53 | 649.23 |
| | 19-6936 | 40.90 | 577.20 | 678.40 |
| 7882 | | 54.70 | 544.83 | 653.78 |
| | 22-6963 | 34.20 | 549.73 | 585.38 |
| | 9-6957 | 31.30 | 488.78 | 531.35 |
| 7886 | | 27.60 | 338.90 | 406.85 |
| | 3-6969 | 29.80 | 452.23 | 577.60 |
| | 22-6963 | 34.20 | 549.73 | 585.38 |
| 7889 | | 33.10 | 565.98 | 671.30 |
| | 16-75081 | 29.30 | 442.23 | 535.73 |
| | 24-75003 | 27.40 | 503.60 | 610.60 |
| 7890 | | 51.80 | 622.48 | 734.10 |
| | 3-75077 | 38.40 | 539.38 | 655.03 |
| | 11-75081 | 35.70 | 551.03 | 648.40 |
| 7899 | | 32.80 | 237.80 | 407.20 |
| | 17-75018 | 24.40 | 374.45 | 663.18 |
| | 1-75092 | 24.00 | 368.95 | 627.85 |
| 78100 | | 34.50 | 437.43 | 671.25 |
| | 1-75092 | 24.00 | 368.95 | 627.85 |
| | 31-75088 | 31.60 | 364.83 | 593.83 |

inferiority of that progeny to its own parents. These estimated differences are presented in Table 3 for 1980 and 1981. The statistical analysis showed that the progenies 7846, 7854, 7858, 7870, 7873, 7882, 7889, 7890, 7899, and 78100 in 1980, and the progenies 7846, 7854, 7856, 7858, 7870, 7873, 7882, 7889, 7890, 7899, and 78100 in 1981, had higher estimated differences. It is obvious that these progenies almost showed the same trend for both seasons, and they were superior to their parents. However, certain progenies were statistically less significant than their own parents. They had lower estimated differences. These progenies were 7810 and 7886 in 1980, while in 1981, they were 7810, 7836, and 7886. There is no doubt that these progenies reflect degrees of inferiority to their parents.

Moreover, the statistical analysis clearly showed that there were no significant differences between some progenies and their parental clones in both growing seasons. These progenies were 7801, 7815, 7836, 7856, 7864, and 7878 in 1980, while in 1981, these progenies were 7801, 7815, 7864, and 7878.

Berry firmness (gms)

The data on the average berry firmness (gms) are presented in Tables 1 and 2 for both progenies and their respective parents in 1980 and 1981 growing seasons. It is clear that data represent the average of berry firmness for all genotypes studied. The average firmness of the berries varied for the progenies and their parental clones in both 1980 and 1981. These averages ranged from 212.85 gms to 707.15 gms for the progenies, and from 363.35 gms to 571.83 gms for the parents in 1980. These averages, however, ranged from 213.65 gms to 709.08 gms and from 364.83 gms to

Table 3. Estimated differences of yield (average number of berries per plant) between each progeny and its parental clones in 1980 and 1981[z]

| Genotypes[y] | | | Estimated difference[x] | |
|---|---|---|---|---|
| Progeny | $Parent_1$ | $Parent_2$ | 1980 | 1981 |
| 7801 | 80-6935 | 6-75123 | 1.10 | 2.45 |
| 7810 | 8-75065 | 42-6943 | -11.80 | -11.00 |
| 7815 | 6-75060 | 25-6943 | 1.45 | 0.35 |
| 7836 | 1-75004 | 25-6943 | - 3.40 | - 4.15 |
| 7846 | 21-6937 | 19-6935 | 13.35 | 13.25 |
| 7854 | 14-6967 | 25-6943 | 13.40 | 12.58 |
| 7856 | 46-6943 | 3-6969 | 3.65 | 3.35 |
| 7858 | 9-6957 | 6-75123 | 13.05 | 12.62 |
| 7864 | 9-7410 | 19-8935 | - 1.65 | - 2.55 |
| 7870 | 13-75060 | 20-6971 | 5.05 | 4.65 |
| 7873 | 19-6935 | 3-6969 | 17.80 | 17.00 |
| 7878 | 16-75056 | 19-6936 | - 1.70 | - 1.55 |
| 7882 | 22-6963 | 9-6957 | 22.55 | 21.95 |
| 7886 | 3-6969 | 22-6963 | - 4.45 | - 4.40 |
| 7889 | 16-75081 | 24-75003 | 5.00 | 4.75 |
| 7890 | 3-75077 | 11-75081 | 14.00 | 14.75 |
| 7899 | 17-75018 | 1-75092 | 8.90 | 8.60 |
| 78100 | 1-75092 | 31-75088 | 6.90 | 6.70 |

[z]Estimated difference = average of the progeny - (average of $Parent_1$ + average of $Parent_2$)/2.

[y]First is female parent; second is male parent.

[x]Significant at .001 level.

577.20 gms for the progenies and the parents, respectively, in 1981. The variations among the progenies, as well as among their parents, and the variations between the progenies and their parental clones were detected using an F-test with P=.001. A wide range of variations for the average berry firmness was observed within the progenies, within their parents, and between the progenies and their parents as well.

In both 1980 and 1981, it was noticed that the ranges of average berry firmness for the parents fell within the ranges of their offspring, which indicates certain progenies were superior and others inferior to their parental clones. Moreover, the differences between genotypes were highly significant, statistically.

To answer the question of specific comparisons of the progenies to their own parental clones, conservative multiple t-test was used. The data appearing in Tables 1 and 2 showed that most progenies were superior to their own parents, and in this regard they showed highly significant differences for average berry firmness from their parents. The difference between the mean of a specific progeny and the average means of its own parents together was estimated. This difference gives an indication whether the progeny was superior or inferior to its parents. The estimated differences are given in Table 4 for 1980 and 1981 growing seasons. Higher estimated differences were obtained by the progenies 7810, 7815, 7836, 7846, 7854, 7856, 7870, 7873, 7878, 7889, 7890 and 78100 in both 1980 and 1981. These progenies, as indicated by the statistical analysis, were superior to their parental clones. In contrast, the progenies 7801, 7858, 7864, 7886, and 7899 were significantly less than their own parental

Table 4. Estimated differences of the average berry firmness (gms) between each progeny and its parental clones in 1980 and 1981[z]

| Progeny | Genotypes[y] | | Estimated difference[x] | |
|---|---|---|---|---|
| | $Parent_1$ | $Parent_2$ | 1980 | 1981 |
| 7801 | 80-6935 | 6-75123 | - 96.85 | -101.13 |
| 7810 | 8-75065 | 42-6943 | 138.46 | 138.08 |
| 7815 | 6-75060 | 25-6943 | 198.94 | 203.23 |
| 7836 | 1-75004 | 25-6943 | 221.76 | 224.08 |
| 7846 | 21-6937 | 19-6935 | 162.98 | 162.93 |
| 7854 | 14-6967 | 25-6943 | 102.43 | 100.06 |
| 7856 | 46-6943 | 3-6969 | 53.18 | 49.99 |
| 7858 | 9-6957 | 6-75123 | - 97.04 | - 86.42 |
| 7864 | 9-7410 | 19-8935 | -263.75 | -264.58 |
| 7870 | 13-75060 | 20-6971 | 52.49 | 54.04 |
| 7873 | 19-6935 | 3-6969 | 141.96 | 143.16 |
| 7878 | 16-75056 | 19-6936 | 85.51 | 86.31 |
| 7882 | 22-6963 | 9-6957 | 23.86 | 25.58 |
| 7886 | 3-6969 | 22-6963 | -159.64 | -162.08 |
| 7889 | 16-75081 | 24-75003 | 94.79 | 93.06 |
| 7890 | 3-75077 | 11-75081 | 74.19 | 77.28 |
| 7899 | 17-75018 | 1-75092 | -148.80 | -133.90 |
| 78100 | 1-75092 | 31-75088 | 72.05 | 70.54 |

[z]Estimated difference = average of the progeny - (average of $Parent_1$ + average of $Parent_2$)/2.

[y]First is female parent; second is male parent.

[x]Significant at .001 level.

clones with regard to the average berry firmness. The results indicated that these five progenies were inferior to their parents in both 1980 and 1981 growing seasons.

The statistical analysis revealed that the progeny 7882 was the only one that showed no significant difference as compared to its own parental clones either in 1980 or in 1981.

Capping force (the force required for berry detachment in gms)

The easy cap trait, "removing the berries with the calyx remaining attached to the plant," was determined as the force required for berry detachment (gms). In comparing the progenies and their parental clones, the data in Tables 1 and 2 for both 1980 and 1981 showed that the average force required for berry detachment was greatly varied among the progenies, among the parents, and between the progenies and their respective parental clones. The ranges of the averages were from 387.70 gms to 772.35 gms for the progenies and from 457.13 gms to 673.83 gms for their parents in 1980, whereas these ranges in 1981 were from 394.55 gms to 772.90 gms and from 451.83 gms to 678.40 gms for the progenies and the parents, respectively. These variations were detected using the F-test with $P = .001$.

Once again, the same situation that was detected for the average berry firmness appeared for the capping force, i.e., the ranges of the average force required for berry detachment for the parental clones fell witnin the ranges of their progenies. The indication of that was certain progenies were superior to their parents for the average force required for berry detachment, whereas some others were inferior. Generally speaking,

it was found that the differences between all genotypes studied were statistically highly significant.

Conservative multiple t-test was used for comparing a given progeny to its two parental clones. The difference between the mean of that progeny and the average means of the two parents together was estimated. The estimated differences of the average force required for berry detachment (gms) between each progeny and its parental clones in 1980 and 1981 are presented in Table 5. In both 1980 and 1981, the expression of the easy cap trait almost followed the same trend. The progenies 7810, 7815, 7836, 7846, 7854, 7873, 7882, 7889, 7890, and 78100 in 1980, and the progenies 7810, 7815, 7836, 7846, 7854, 7873, 7882, 7889, 7890 in 1981, showed higher significant differences as compared to their own parents. However, the progenies 7801, 7858, 7864, 7886, and 7899 were statistically less significant as compared to their own parental clones and showed negative estimated differences which reflect the inferiority of these progenies to their parents.

The statistical analysis of the data about the easy cap trait that was given in Tables 1 and 2 and the estimated differences that are presented in Table 5 showed there were no such significant differences between some progenies and their own parents. These progenies were 7856, 7870, and 7878 in 1980, whereas they were 7856, 7870, 7878, and 78100 for the 1981 growing season.

Table 5. Estimated differences of the average force required for berry detachment (gms) between each progeny and its parental clones in 1980 and 1981[z]

| Genotypes[y] | | | Estimated difference[x] | |
|---|---|---|---|---|
| Progeny | $Parent_1$ | $Parent_2$ | 1980 | 1981 |
| 7801 | 80-6935 | 6-75123 | -106.25 | -103.80 |
| 7810 | 8-75065 | 42-6943 | 155.78 | 158.91 |
| 7815 | 6-75060 | 25-6943 | 119.01 | 117.68 |
| 7836 | 1-75004 | 25-6943 | 76.39 | 81.76 |
| 7846 | 21-6937 | 19-6935 | 214.90 | 225.60 |
| 7854 | 14-6967 | 25-6943 | 132.99 | 132.26 |
| 7856 | 46-6943 | 3-6969 | 31.28 | 26.86 |
| 7858 | 9-6957 | 6-75123 | - 85.85 | - 71.33 |
| 7864 | 9-7410 | 19-8935 | -121.00 | -116.75 |
| 7870 | 13-75060 | 20-6971 | 48.44 | 46.38 |
| 7873 | 19-6935 | 3-6969 | 143.93 | 147.69 |
| 7878 | 16-75056 | 19-6936 | 30.11 | 38.44 |
| 7882 | 22-6963 | 9-6957 | 91.43 | 94.91 |
| 7886 | 3-6969 | 22-6963 | -169.50 | -174.64 |
| 7889 | 16-75081 | 24-75003 | 99.11 | 98.14 |
| 7890 | 3-75077 | 11-75081 | 82.45 | 82.39 |
| 7899 | 17-75018 | 1-75092 | -260.95 | -238.31 |
| 78100 | 1-75092 | 31-75088 | 63.18 | 60.41 |

[z]Estimated difference = average of the progeny - (average of $Parent_1$ + average of $Parent_2$) / 2 .

[y]First is female parent; second is male parent.

[x]Significant at .001 level.

## Changes of the Characters during the Four Harvesting Periods

### Percent of ripe berries per harvest (concentrated ripening)

The percentages of mature berries per harvest for 1980 and 1981 seasons are presented in Tables 6 and 7 and illustrated in Figure 1 for the progenies and their parental clones. It was noticed that almost all genotypes studied tended to concentrate their ripening through the second and third harvesting periods in both growing seasons. In 1980, the percentages of ripe berries during the first harvesting period ranged from 6 to 23 for the progenies and from 6 to 25 for their parental clones. In the second harvesting period, the percentages were from 31 to 47 and from 24 to 46 for the progenies and their parents, respectively. During the third harvesting period, the percentages of ripe berries were almost the same as that of the second period; these percentages ranged from 25 to 43 for the progenies and from 25 to 41 for the parents. In the last harvesting period, the percentages ranged from 5 to 21 and from 7 to 23 for the progenies and their parents, respectively.

As a general rule, the first and fourth harvesting periods together represented about 11% to 44% of the ripe berries, whereas the second and the third periods together represented 56% to 89% for the progenies. As most of the parental clones followed the same trend, the percentages of ripe berries during the first and fourth periods ranged from 13 to 48, while, during the second and third harvesting periods, these percentages ranged from 52 to 87.

Table 6. Changes of the average number of berries per plant during harvesting periods for the progenies and their parental clones in 1980[z]

| Genotypes | | Harvests | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | $H_1$ | | $H_2$ | | $H_3$ | | $H_4$ | |
| Progenies | Parents[y] | No. | % | No. | % | No. | % | No. | % |
| 7801 | | 3.8 | 11 | 13.2 | 40 | 12.6 | 38 | 3.7 | 11 |
| | 80-6935 | 3.6 | 12 | 11.5 | 38 | 11.6 | 38 | 3.7 | 12 |
| | 6-75123 | 3.8 | 11 | 13.8 | 41 | 12.6 | 37 | 3.8 | 11 |
| 7810 | | 3.3 | 9 | 14.5 | 41 | 14.1 | 40 | 3.5 | 10 |
| | 8-75065 | 3.4 | 9 | 18.2 | 41 | 17.9 | 40 | 4.2 | 10 |
| | 42-6943 | 3.7 | 7 | 22.3 | 44 | 19.7 | 40 | 4.5 | 9 |
| 7815 | | 7.0 | 23 | 9.1 | 31 | 7.6 | 25 | 6.1 | 21 |
| | 6-75060 | 6.6 | 25 | 7.4 | 29 | 6.6 | 25 | 5.6 | 21 |
| | 25-6943 | 3.4 | 11 | 12.0 | 40 | 12.0 | 39 | 3.1 | 10 |
| 7836 | | 5.6 | 18 | 9.3 | 34 | 8.3 | 31 | 4.7 | 17 |
| | 1-75004 | 6.0 | 20 | 10.1 | 32 | 9.2 | 30 | 5.6 | 18 |
| | 25-6943 | 3.4 | 11 | 12.0 | 40 | 12.0 | 39 | 3.1 | 10 |
| 7846 | | 3.4 | 6 | 26.8 | 45 | 26.0 | 43 | 3.6 | 6 |
| | 21-6937 | 3.6 | 6 | 27.6 | 46 | 24.8 | 41 | 3.8 | 7 |
| | 19-6935 | 3.0 | 9 | 14.9 | 45 | 12.4 | 37 | 2.8 | 9 |
| 7854 | | 4.2 | 10 | 18.7 | 43 | 17.3 | 39 | 3.4 | 8 |
| | 14-6967 | 4.0 | 14 | 13.2 | 44 | 9.7 | 32 | 3.0 | 10 |
| | 25-6943 | 3.4 | 11 | 12.0 | 40 | 12.0 | 39 | 3.1 | 10 |
| 7856 | | 3.5 | 10 | 14.0 | 41 | 13.2 | 39 | 3.3 | 10 |
| | 46-6943 | 5.8 | 19 | 10.4 | 33 | 8.7 | 28 | 6.3 | 20 |
| | 3-6969 | 3.6 | 12 | 12.2 | 41 | 10.5 | 36 | 3.2 | 11 |
| 7858 | | 4.2 | 9 | 19.7 | 44 | 17.0 | 38 | 4.2 | 9 |
| | 9-6957 | 3.3 | 11 | 12.1 | 40 | 11.3 | 38 | 3.4 | 11 |
| | 6-75123 | 3.8 | 11 | 13.8 | 41 | 12.6 | 37 | 3.8 | 11 |
| 7864 | | 3.3 | 11 | 11.7 | 41 | 10.4 | 36 | 3.3 | 12 |
| | 9-7410 | 3.7 | 13 | 11.0 | 40 | 9.2 | 34 | 3.7 | 13 |
| | 19-6935 | 3.0 | 9 | 14.9 | 45 | 12.4 | 37 | 2.8 | 9 |

[z]Each figure represents the average of the two replications.

[y]Upper figure is female parent; lower figure is male parent.

Table 6. *Continued*

| Genotypes | | Harvests | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | $H_1$ | | $H_2$ | | $H_3$ | | $H_4$ | |
| Progenies | Parents[y] | No. | % | No. | % | No. | % | No. | % |
| 7870 | | 3.3 | 11 | 12.7 | 41 | 11.6 | 37 | 3.5 | 11 |
| | 13-75060 | 3.5 | 13 | 10.1 | 37 | 10.2 | 38 | 3.2 | 12 |
| | 20-6971 | 3.6 | 14 | 9.2 | 37 | 8.9 | 35 | 3.4 | 14 |
| 7873 | | 3.1 | 6 | 22.1 | 45 | 20.5 | 42 | 3.4 | 7 |
| | 19-6935 | 3.0 | 9 | 14.9 | 45 | 12.4 | 37 | 2.8 | 9 |
| | 3-6969 | 3.6 | 12 | 12.2 | 41 | 10.5 | 36 | 3.2 | 11 |
| 7878 | | 3.2 | 9 | 14.7 | 41 | 14.6 | 41 | 3.2 | 9 |
| | 16-75056 | 3.4 | 10 | 13.9 | 41 | 13.4 | 39 | 3.4 | 10 |
| | 19-6936 | 3.6 | 9 | 17.1 | 42 | 16.4 | 40 | 3.6 | 9 |
| 7882 | | 4.3 | 8 | 23.9 | 44 | 22.3 | 41 | 4.1 | 7 |
| | 22-6963 | 3.3 | 9 | 13.9 | 41 | 13.2 | 39 | 3.6 | 11 |
| | 9-6957 | 3.3 | 11 | 12.1 | 40 | 11.3 | 38 | 2.4 | 11 |
| 7886 | | 3.7 | 14 | 10.4 | 38 | 9.7 | 35 | 3.5 | 13 |
| | 3-6969 | 3.6 | 12 | 12.2 | 41 | 10.5 | 36 | 3.2 | 11 |
| | 22-6963 | 3.3 | 9 | 13.9 | 41 | 13.2 | 39 | 3.6 | 11 |
| 7889 | | 3.8 | 12 | 13.6 | 40 | 12.2 | 36 | 4.0 | 12 |
| | 16-75081 | 3.3 | 11 | 11.7 | 39 | 11.5 | 38 | 3.4 | 12 |
| | 24-75003 | 3.4 | 13 | 10.7 | 39 | 10.1 | 37 | 3.1 | 11 |
| 7890 | | 2.8 | 6 | 23.8 | 47 | 21.7 | 42 | 2.7 | 5 |
| | 3-75077 | 2.9 | 8 | 16.9 | 44 | 15.3 | 40 | 3.2 | 8 |
| | 11-75081 | 3.5 | 10 | 14.4 | 40 | 14.3 | 40 | 3.5 | 10 |
| 7899 | | 2.5 | 8 | 13.9 | 42 | 13.4 | 41 | 2.9 | 9 |
| | 17-75018 | 4.5 | 18 | 7.9 | 32 | 7.4 | 30 | 4.8 | 20 |
| | 1-75092 | 3.9 | 17 | 7.9 | 34 | 7.1 | 31 | 4.1 | 18 |
| 78100 | | 4.5 | 13 | 13.3 | 39 | 12.5 | 37 | 3.8 | 11 |
| | 1-75092 | 3.9 | 17 | 7.9 | 34 | 7.1 | 31 | 4.1 | 18 |
| | 31-75088 | 7.5 | 24 | 7.6 | 24 | 9.0 | 29 | 7.3 | 23 |

Table 7. Changes in the average number of berries per plant during harvesting periods for the progenies and their parental clones in 1981[z]

| Genotypes | | Harvests | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | $H_1$ | | $H_2$ | | $H_3$ | | $H_4$ | |
| Progenies | Parents[y] | No. | % | No. | % | No. | % | No. | % |
| 7801 | | 3.5 | 10 | 13.5 | 40 | 13.0 | 38 | 4.0 | 12 |
| | 80-6935 | 3.7 | 12 | 11.6 | 39 | 11.3 | 38 | 3.3 | 11 |
| | 6-75123 | 3.8 | 11 | 12.8 | 39 | 12.8 | 39 | 3.8 | 11 |
| 7810 | | 3.5 | 10 | 14.3 | 40 | 14.4 | 40 | 3.5 | 10 |
| | 8-75065 | 4.0 | 9 | 18.0 | 41 | 17.6 | 41 | 3.8 | 9 |
| | 42-6943 | 4.3 | 9 | 21.6 | 43 | 20.0 | 40 | 4.1 | 8 |
| 7815 | | 6.9 | 24 | 8.7 | 30 | 7.4 | 25 | 6.2 | 21 |
| | 6-75060 | 6.5 | 25 | 7.8 | 30 | 6.5 | 24 | 5.7 | 21 |
| | 25-6943 | 3.7 | 12 | 12.4 | 40 | 12.0 | 38 | 3.1 | 10 |
| 7836 | | 4.8 | 18 | 10.0 | 36 | 7.7 | 29 | 4.7 | 17 |
| | 1-75004 | 6.1 | 20 | 11.1 | 35 | 8.3 | 26 | 6.0 | 19 |
| | 25-6943 | 3.7 | 12 | 12.4 | 40 | 12.0 | 38 | 3.1 | 10 |
| 7846 | | 3.8 | 7 | 26.5 | 44 | 25.9 | 43 | 3.5 | 6 |
| | 21-6937 | 3.6 | 6 | 27.4 | 45 | 25.4 | 42 | 3.9 | 7 |
| | 19-6935 | 3.2 | 10 | 13.4 | 41 | 13.2 | 41 | 2.8 | 8 |
| 7854 | | 3.6 | 8 | 18.3 | 42 | 17.6 | 41 | 3.9 | 9 |
| | 14-6967 | 4.3 | 15 | 12.0 | 40 | 10.8 | 36 | 2.8 | 9 |
| | 25-6943 | 3.7 | 12 | 12.4 | 40 | 12.0 | 38 | 3.1 | 10 |
| 7856 | | 3.5 | 10 | 14.3 | 42 | 12.8 | 38 | 3.2 | 10 |
| | 46-6943 | 6.2 | 20 | 10.3 | 33 | 9.0 | 29 | 5.6 | 18 |
| | 3-6969 | 3.7 | 13 | 11.7 | 39 | 11.0 | 37 | 3.4 | 11 |
| 7858 | | 3.9 | 9 | 19.9 | 42 | 17.7 | 40 | 4.2 | 9 |
| | 9-6957 | 3.7 | 12 | 12.5 | 40 | 11.7 | 37 | 3.4 | 11 |
| | 6-75123 | 3.8 | 11 | 12.8 | 39 | 12.8 | 39 | 3.8 | 11 |
| 7864 | | 3.3 | 12 | 11.7 | 42 | 10.0 | 36 | 2.8 | 10 |
| | 9-7410 | 3.9 | 14 | 11.0 | 39 | 9.5 | 34 | 3.7 | 13 |
| | 19-6935 | 3.2 | 10 | 13.4 | 41 | 13.2 | 41 | 2.8 | 8 |

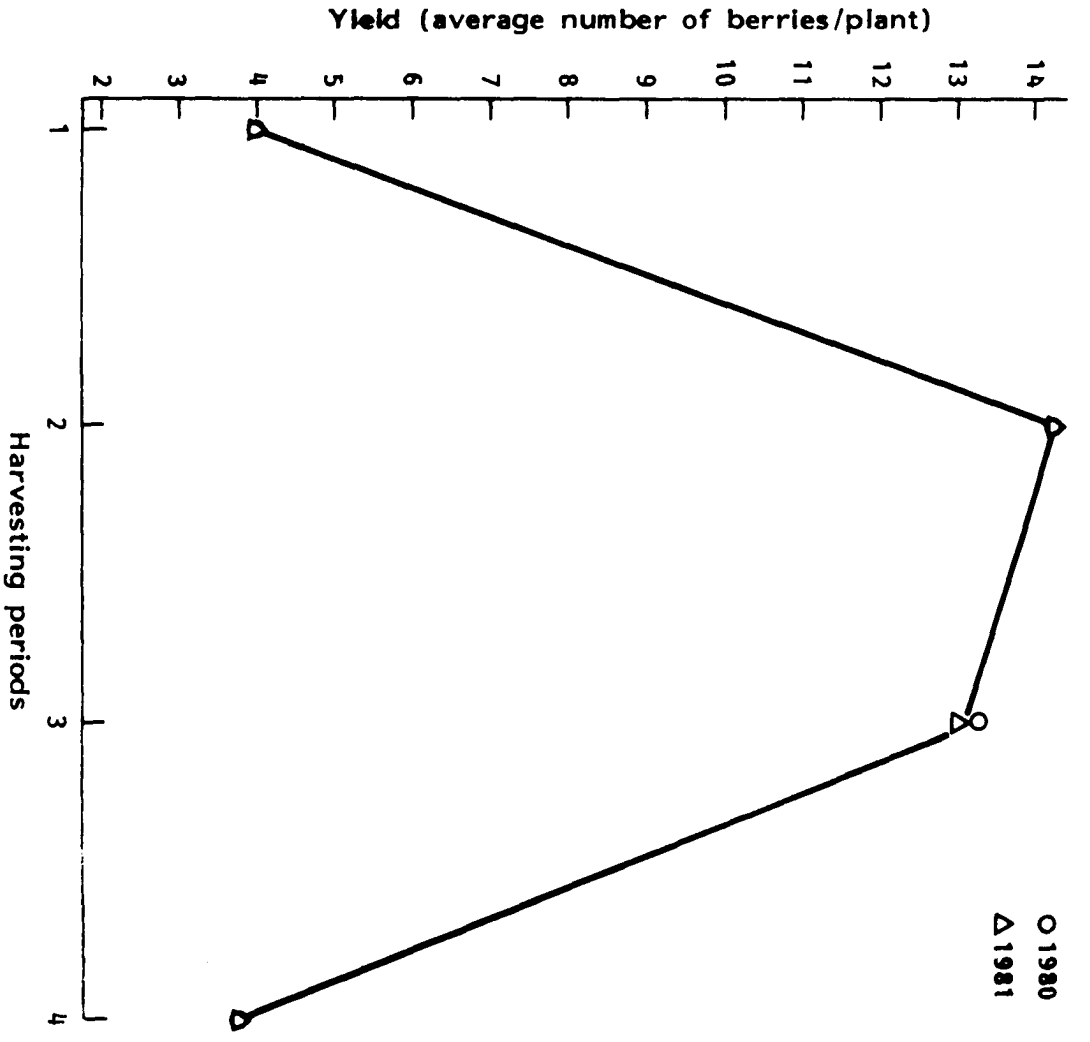
[z]Each figure represents the average of the two replications.

[y]Upper figure is female parent; lower is male parent.

Table 7. *Continued*

| Genotypes | | Harvests | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | $H_1$ | | $H_2$ | | $H_3$ | | $H_4$ | |
| Progenies | Parents[y] | No. | % | No. | % | No. | % | No. | % |
| 7870 | | 3.3 | 11 | 12.5 | 40 | 11.8 | 38 | 3.4 | 11 |
| | 13-75060 | 3.4 | 13 | 11.0 | 42 | 8.9 | 33 | 3.1 | 12 |
| | 20-6971 | 3.6 | 14 | 10.7 | 40 | 8.1 | 31 | 3.9 | 15 |
| 7873 | | 3.0 | 7 | 22.3 | 46 | 20.0 | 41 | 2.9 | 6 |
| | 19-6935 | 3.2 | 10 | 13.4 | 41 | 13.2 | 41 | 2.8 | 8 |
| | 3-6969 | 3.7 | 13 | 11.7 | 39 | 11.0 | 37 | 3.4 | 11 |
| 7878 | | 3.6 | 11 | 14.8 | 41 | 14.1 | 39 | 3.3 | 9 |
| | 16-75056 | 3.7 | 11 | 13.4 | 40 | 13.5 | 40 | 3.2 | 9 |
| | 19-6936 | 3.8 | 9 | 17.5 | 43 | 15.8 | 39 | 3.8 | 9 |
| 7882 | | 4.1 | 8 | 23.7 | 43 | 22.5 | 41 | 4.4 | 8 |
| | 22-6963 | 3.7 | 11 | 13.8 | 40 | 13.3 | 39 | 3.4 | 10 |
| | 9-6957 | 3.7 | 12 | 12.5 | 40 | 11.7 | 37 | 3.4 | 11 |
| 7886 | | 3.7 | 13 | 11.7 | 42 | 8.7 | 32 | 3.5 | 13 |
| | 3-6969 | 3.7 | 13 | 11.7 | 39 | 11.0 | 37 | 3.4 | 11 |
| | 22-6963 | 3.7 | 11 | 13.8 | 40 | 13.3 | 39 | 3.4 | 10 |
| 7889 | | 4.0 | 12 | 13.5 | 41 | 11.6 | 35 | 4.0 | 12 |
| | 16-75081 | 3.3 | 11 | 11.7 | 40 | 11.1 | 38 | 3.2 | 11 |
| | 24-75003 | 3.3 | 12 | 11.3 | 41 | 9.5 | 35 | 3.3 | 12 |
| 7890 | | 2.8 | 5 | 24.7 | 48 | 21.3 | 41 | 3.0 | 6 |
| | 3-75077 | 3.0 | 8 | 16.9 | 44 | 15.5 | 40 | 3.0 | 8 |
| | 11-75081 | 3.7 | 10 | 14.8 | 41 | 13.8 | 39 | 3.4 | 10 |
| 7899 | | 3.5 | 11 | 13.1 | 40 | 12.8 | 39 | 3.4 | 10 |
| | 17-75018 | 5.1 | 21 | 8.0 | 33 | 7.3 | 30 | 4.0 | 16 |
| | 1-75092 | 5.0 | 21 | 7.5 | 31 | 7.1 | 30 | 4.4 | 18 |
| 78100 | | 4.6 | 14 | 13.5 | 39 | 11.9 | 34 | 4.5 | 13 |
| | 1-75092 | 5.0 | 21 | 7.5 | 31 | 7.1 | 30 | 4.4 | 18 |
| | 31-75088 | 8.1 | 26 | 8.5 | 27 | 7.6 | 24 | 7.4 | 23 |

Figure 1. Changes in the yield (the average number of berries per plant) during the four harvesting periods for both progenies and their parental clones in the 1980 and 1981 growing seasons


Yield (average number of berries/plant)
2
3
4
5
6
7
8
9
10
11
12
13
14
Harvesting periods
1
2
3
4
○ 1980
△ 1981

It was evident from the data given in Table 7, for the 1981 season, that the second and third harvesting periods represented the maximum percentages of ripe berries for almost all the entities, while the first, as well as the fourth, periods gave the minimum percentages. During the first harvesting period, the progenies showed about 7% to 24% ripe berries as compared to 6% to 26% for their parental clones. In the second harvesting period, the percentages were 30 to 48 for the progenies and 30 to 45 for the parents. The same trend was found in the third harvesting period as that obtained in the second; the percentages of ripe berries ranged from 25 to 43 and from 24 to 42 for the progenies and the parents, respectively.

Once again, the first and fourth harvesting periods in 1981 had lower percentages of ripe berries, ranging from 11 to 45 and from 13 to 46 for the progenies and the parents, respectively. In the second and third periods, the progenies produced 55% to 89%, as compared to 54% to 87% for the parental clones.

All these data indicate that there were significant differences between the four harvesting periods with regard to the percentage of ripe berries for each period. To get an accurate judgement about the significance between the four harvesting periods, the Tukey test was used. This test indicated that there was an entity-harvest interaction which was significant at .001; and it was such that a ranking of harvest means indicated which harvest periods were superior. According to this statistical analysis, it was found that means of the numerical numbers of berries during the four harvesting periods in 1980 for the forty-four entities were

3.94, 14.17, 13.14, and 3.87, which represent 11.2%, 40.3%, 37.4%, and 11.1% for the first, second, third, and fourth harvesting periods.

In 1981, these means were 4.09, 14.20, 13.00, and 3.86, which represent 11.6%, 40.4%, 37.0%, and 11.0% for the four harvesting periods. It was clear as indicated from the data in Tables 6 and 7, and as shown in Figure 1, that the percentages of ripe berries for most of the genotypes reached the peak during the second and the third harvesting periods. Moreover, partitioning the harvest's sum of squares into linear, quadratic and lack of fit indicated that the quadratic sum of squares was highly significant at P=.001 level. Hence, the relationship between the four harvesting periods and the percentages of ripe berries appeared to be quadratic. This result strongly supports the changes of the percentages of ripe berries throughout the four harvests.

Berry firmness (gms)

The data on changes of the average berry firmness (gms) during the four harvesting periods for the progenies and their parental clones in 1980 and 1981 are presented in Tables 8 and 9 and shown in Figure 2. It was found that average berry firmness decreased with the progression of the harvesting periods for almost all genotypes studied. In 1980, the progeny 7899 gave the lowest average berry firmness throughout the four harvesting periods. These averages were 236.50, 243.00, 219.30, and 194.40 gms, as compared to the highest averages given by the progeny 7815 of 774.60, 722.90, 691.50, and 666.60 gms for first, second, third and fourth harvesting periods, respectively.

Table 8. Changes in average berry firmness (gms) during harvesting periods for the progenies and their parental clones in 1980[z]

| Genotypes | | Harvests | | | |
|---|---|---|---|---|---|
| Progenies | Parents[y] | $H_1$ | $H_2$ | $H_3$ | $H_4$ |
| 7801 | | 400.90 | 382.20 | 363.80 | 337.20 |
| | 80-6935 | 584.20 | 562.60 | 539.00 | 518.30 |
| | 6-75123 | 413.70 | 395.30 | 379.90 | 353.00 |
| 7810 | | 608.70 | 584.40 | 568.80 | 547.50 |
| | 8-75065 | 475.40 | 462.50 | 441.40 | 422.20 |
| | 42-6943 | 452.80 | 437.10 | 417.70 | 402.00 |
| 7815 | | 747.60 | 722.90 | 691.50 | 666.60 |
| | 6-75060 | 587.30 | 564.60 | 539.70 | 522.50 |
| | 25-6943 | 491.00 | 471.00 | 453.50 | 436.10 |
| 7836 | | 683.20 | 664.60 | 647.90 | 634.60 |
| | 1-75004 | 428.90 | 415.30 | 403.20 | 387.50 |
| | 25-6943 | 491.00 | 471.00 | 453.50 | 436.10 |
| 7846 | | 669.80 | 644.00 | 624.90 | 616.80 |
| | 21-6937 | 557.20 | 530.50 | 503.00 | 481.60 |
| | 19-6935 | 455.50 | 442.80 | 426.00 | 410.60 |
| 7854 | | 596.90 | 587.50 | 576.80 | 564.00 |
| | 14-6967 | 505.40 | 500.70 | 493.10 | 480.20 |
| | 25-6943 | 491.00 | 471.00 | 453.50 | 436.10 |
| 7856 | | 502.50 | 496.10 | 487.80 | 471.30 |
| | 46-6943 | 443.30 | 425.20 | 412.10 | 397.40 |
| | 3-6969 | 473.10 | 458.90 | 444.40 | 434.80 |
| 7858 | | 364.30 | 348.10 | 334.40 | 316.30 |
| | 9-6957 | 508.90 | 495.50 | 484.10 | 475.10 |
| | 6-75123 | 413.70 | 395.30 | 376.90 | 353.00 |

[z]Each figure represents the average of the two replications.

[y]Upper figure is female parent; lower figure is male parent.

Table 8. *Continued*

| Genotypes | | Harvests | | | |
|---|---|---|---|---|---|
| Progenies | Parents[y] | $H_1$ | $H_2$ | $H_3$ | $H_4$ |
| 7864 | | 240.30 | 217.60 | 202.90 | 190.60 |
| | 9-7410 | 541.00 | 525.70 | 513.10 | 498.10 |
| | 19-6935 | 455.50 | 442.80 | 426.00 | 410.60 |
| 7870 | | 528.10 | 530.70 | 510.80 | 489.50 |
| | 13-75060 | 500.00 | 490.70 | 471.80 | 459.30 |
| | 20-6971 | 466.90 | 451.00 | 434.50 | 424.10 |
| 7873 | | 609.60 | 594.30 | 578.20 | 558.80 |
| | 19-6935 | 455.50 | 442.80 | 426.00 | 410.60 |
| | 3-6969 | 473.10 | 458.90 | 444.40 | 434.80 |
| 7878 | | 643.50 | 633.10 | 622.10 | 605.30 |
| | 16-75056 | 532.80 | 516.90 | 500.60 | 486.30 |
| | 19-6936 | 593.00 | 579.10 | 564.30 | 550.90 |
| 7882 | | 566.80 | 552.80 | 539.10 | 518.10 |
| | 22-6963 | 571.70 | 554.20 | 542.80 | 530.40 |
| | 9-6957 | 508.90 | 495.50 | 484.10 | 475.10 |
| 7886 | | 375.10 | 357.70 | 331.60 | 302.20 |
| | 3-6969 | 473.10 | 458.90 | 444.40 | 434.80 |
| | 22-6963 | 571.70 | 554.20 | 542.80 | 530.40 |
| 7889 | | 608.60 | 573.80 | 550.20 | 533.30 |
| | 16-75081 | 468.20 | 448.70 | 430.50 | 413.20 |
| | 24-75003 | 524.40 | 510.10 | 497.10 | 481.30 |
| 7890 | | 655.80 | 633.60 | 608.60 | 585.10 |
| | 3-75077 | 558.10 | 551.30 | 534.20 | 527.20 |
| | 11-75081 | 579.10 | 565.00 | 539.90 | 517.90 |
| 7899 | | 236.50 | 243.00 | 219.30 | 194.40 |
| | 17-75018 | 404.20 | 386.60 | 365.40 | 342.20 |
| | 1-75092 | 394.30 | 383.20 | 358.40 | 326.50 |
| 78100 | | 471.90 | 453.80 | 424.20 | 396.20 |
| | 1-75092 | 394.30 | 383.20 | 358.40 | 326.50 |
| | 31-75098 | 385.20 | 371.30 | 362.40 | 334.50 |

Table 9. Changes in average berry firmness (gms) during harvesting periods for the progenies and their parental clones in 1981[z]

| Genotypes | | Harvests | | | |
|---|---|---|---|---|---|
| Progenies | Parents[y] | $H_1$ | $H_2$ | $H_3$ | $H_4$ |
| 7801 | | 401.30 | 379.90 | 353.90 | 330.40 |
| | 80-6935 | 586.20 | 559.30 | 544.00 | 523.10 |
| | 6-75123 | 415.00 | 396.90 | 370.40 | 345.10 |
| 7810 | | 606.90 | 586.30 | 566.90 | 554.70 |
| | 8-75065 | 478.40 | 466.10 | 443.40 | 422.20 |
| | 42-6943 | 452.40 | 432.80 | 423.70 | 406.00 |
| 7815 | | 747.20 | 722.30 | 694.70 | 672.10 |
| | 6-75060 | 586.00 | 561.20 | 536.70 | 522.50 |
| | 25-6943 | 486.30 | 471.20 | 449.90 | 433.00 |
| 7836 | | 682.50 | 665.10 | 651.20 | 636.10 |
| | 1-75004 | 430.00 | 414.20 | 404.20 | 388.40 |
| | 25-6943 | 486.30 | 471.20 | 449.90 | 433.00 |
| 7846 | | 670.00 | 645.40 | 630.00 | 610.50 |
| | 21-6937 | 557.00 | 529.80 | 503.80 | 486.80 |
| | 19-6935 | 455.00 | 442.70 | 427.10 | 406.20 |
| 7854 | | 595.80 | 583.60 | 569.50 | 553.90 |
| | 14-6967 | 505.40 | 497.30 | 485.70 | 476.30 |
| | 25-6943 | 486.30 | 471.20 | 449.90 | 433.00 |
| 7856 | | 502.20 | 491.90 | 480.90 | 466.20 |
| | 46-6943 | 441.10 | 426.10 | 409.50 | 346.90 |
| | 3-6969 | 473.60 | 459.50 | 446.00 | 429.80 |
| 7858 | | 367.67 | 356.67 | 340.33 | 323.56 |
| | 9-6957 | 508.10 | 494.90 | 481.60 | 470.50 |
| | 6-75123 | 415.00 | 396.90 | 370.40 | 345.10 |

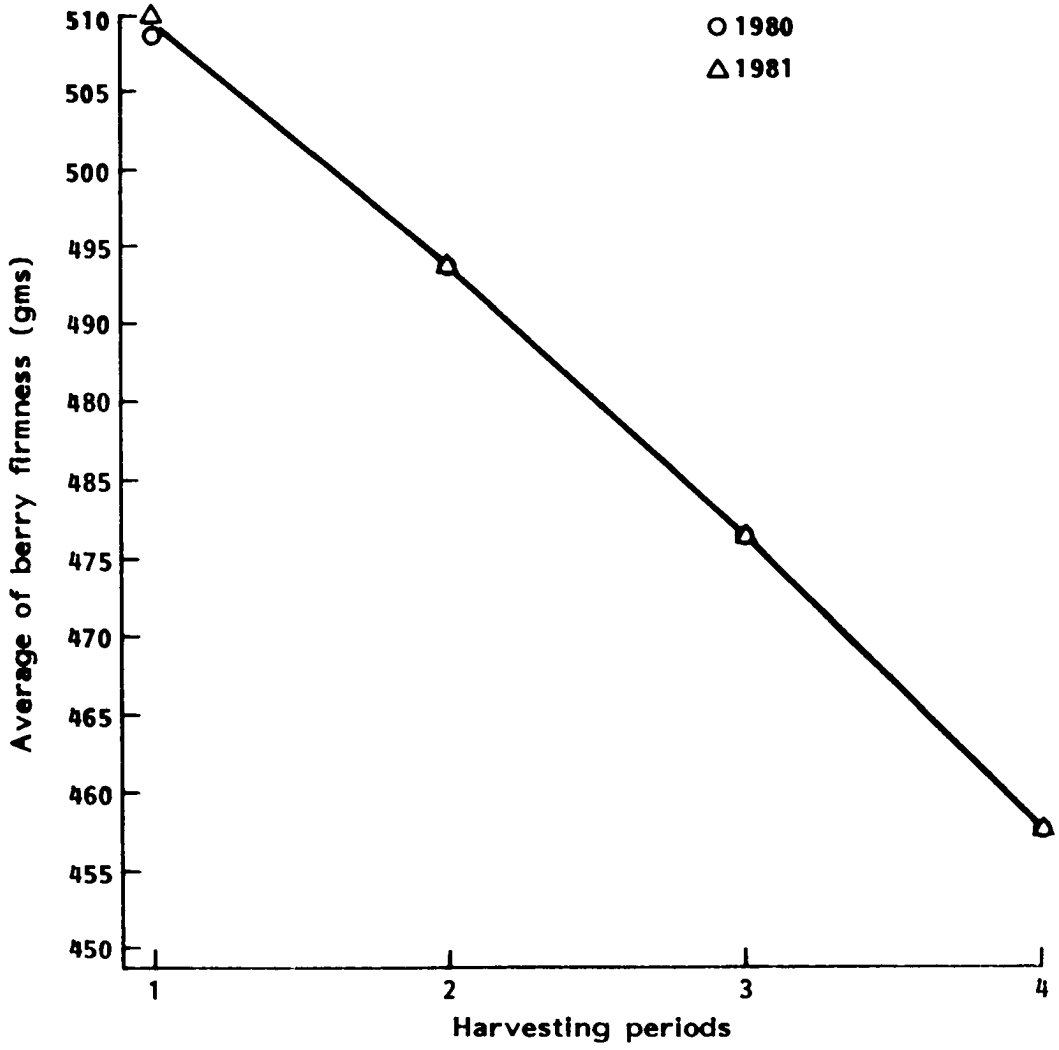
[z]Each figure represents the average of the two replications.

[y]Upper figure is female parent; lower figure is male parent.

Table 9. *Continued*

| Genotypes | | Harvests | | | |
|---|---|---|---|---|---|
| Progenies | Parents[y] | $H_1$ | $H_2$ | $H_3$ | $H_4$ |
| 7864 | | 241.30 | 222.80 | 202.60 | 187.90 |
| | 9-7410 | 542.90 | 531.50 | 517.20 | 503.20 |
| | 19-6935 | 455.00 | 442.70 | 427.10 | 406.20 |
| 7870 | | 529.20 | 525.20 | 509.80 | 488.30 |
| | 13-75060 | 498.50 | 483.90 | 468.40 | 453.80 |
| | 20-6971 | 468.00 | 446.60 | 433.30 | 420.20 |
| 7873 | | 609.40 | 595.20 | 578.40 | 559.60 |
| | 19-6935 | 455.00 | 442.70 | 427.10 | 406.20 |
| | 3-6969 | 473.60 | 495.50 | 446.00 | 429.80 |
| 7878 | | 646.10 | 646.70 | 624.20 | 603.70 |
| | 16-75056 | 531.30 | 516.80 | 507.30 | 486.70 |
| | 19-6936 | 596.10 | 583.50 | 570.80 | 558.40 |
| 7882 | | 566.80 | 552.30 | 538.10 | 522.10 |
| | 22-6963 | 571.70 | 557.70 | 542.30 | 527.20 |
| | 9-6957 | 508.10 | 494.90 | 481.60 | 470.50 |
| 7886 | | 376.00 | 352.80 | 326.10 | 300.70 |
| | 3-6969 | 473.60 | 459.50 | 446.00 | 429.80 |
| | 22-6963 | 571.70 | 557.70 | 542.30 | 527.20 |
| 7889 | | 608.80 | 572.50 | 550.50 | 532.10 |
| | 16-75081 | 474.40 | 446.80 | 431.70 | 416.00 |
| | 24-75003 | 525.00 | 511.60 | 497.40 | 480.40 |
| 7890 | | 655.20 | 637.70 | 611.00 | 586.00 |
| | 3-75077 | 557.60 | 548.00 | 533.20 | 518.70 |
| | 11-75081 | 577.10 | 562.70 | 541.40 | 522.90 |
| 7899 | | 262.90 | 248.10 | 231.70 | 208.50 |
| | 17-75018 | 402.60 | 383.90 | 366.90 | 344.40 |
| | 1-75092 | 396.20 | 382.70 | 361.70 | 335.20 |
| 78100 | | 467.80 | 452.20 | 426.40 | 403.30 |
| | 1-75092 | 396.20 | 382.70 | 361.70 | 335.20 |
| | 31-75088 | 386.20 | 370.50 | 365.60 | 337.00 |

Figure 2. Changes in the average berry firmness (gms) during the four harvesting periods for both progenies and parental clones in the 1980 and 1981 growing seasons


○ 1980
△ 1981
510
505
500
495
490
480
485
475
470
465
460
455
450
Average of berry firmness (gms)
1
2
3
4
Harvesting periods

Also, the same phenomenon was apparent for the parental clones. The averages of berry firmness for the parent 1-75092 were 394.30, 383.20, 358.40 and 326.50 gms for the four harvesting periods, respectively, whereas the averages of berry firmness given by the firmest parent, 19-6936, were 593.00, 579.10, 564.30, and 550.90 gms.

In 1981, the same trends have been observed for both progenies and their parents. The progeny 7864 gave the averages in berry firmness as 241.30, 222.80, 202.60, and 187.90 gms, while the firmest progeny, 7815, gave the averages as 747.20, 722.30, 694.70 and 672.10 gms for the four harvesting periods, respectively. Also, the parent 31-75088 gave the averages of 386.20, 370.50, 365.60, and 337.00 gms, and the parent 19-6936 had averages of 596.10, 583.50, 570.80, and 558.40 gms for the first, second, third, and fourth harvesting periods.

It was obvious from the data appearing in Tables 8 and 9 and the illustration in Figure 2 that the average of berry firmness varies greatly from one period to the other. Also, these averages decreased with the progression of the harvesting periods. The statistical analysis using the Tukey test indicated that the entity-harvest interaction was significant at .001 and allowed the ranking of harvest means. The ranking of average berry firmness during the four harvesting periods in 1980 and 1981 indicated that firmness of the berry decreased with the progression of the harvesting times. The ranking for the average berry firmness for all the forty-four entities in 1980 was 509.22, 493.55, 475.72, and 457.75 gms, whereas in 1981, these averages were 510.03, 493.58, 476.16, and 457.99 gms for the four harvesting times, respectively. Also, partitioning

the harvest's sum of squares into linear and lack of fit indicated that the relationship between the four harvests and the average berry firmness appeared to be linearly significant at P = .001.

Capping force (force required for berry detachment (gms))

The data in Tables 10 and 11 represent the changes in the average force required for berry detachment (gms) for the progenies and their parental clones during the four harvesting periods in 1980 and 1981. Figure 3 clearly shows that the average of the force required for berry detachment decreased from the first through the fourth harvesting periods for all the genotypes studied. In 1980, the lowest averages were given by the progeny 7899; these averages were 396.30, 414.50, 385.70, and 354.30 gms for the four harvesting periods, respectively. The highest averages were 825.80, 785.60, 754.40, and 723.60 gms, which were obtained by the progeny 7815 for the four harvesting periods.

As seen before for the average berry firmness, the parental clones tended to follow the same direction for the average force required for berry detachment. The average capping force for the lowest parental clone, 19-6935, was 489.10, 462.60, 447.20, and 429.60 gms, while the parent 6-75060 gave the highest averages, 719.60, 686.30, 654.60, and 622.50 gms for the four harvesting times.

In 1981, slight differences took place in that the progeny 7864 gave the lowest average capping force instead of progeny 7899, as in 1980. Also, the progeny 7815 and the parents 19-6935 and 6-75060 followed the same trend as that obtained in the 1980 growing season. It was evident that the averages of capping force were greatly different between the four

Table 10. Changes in average capping force (force required for berry detachment in gms) for the progenies and their parental clones in 1980[z]

| Genotypes | | Harvests | | | |
|---|---|---|---|---|---|
| Progenies | Parents[y] | $H_1$ | $H_2$ | $H_3$ | $H_4$ |
| 7801 | | 515.80 | 474.00 | 440.40 | 412.90 |
| | 80-6935 | 690.50 | 675.50 | 626.40 | 594.50 |
| | 6-75123 | 527.30 | 507.60 | 476.80 | 453.80 |
| 7810 | | 754.10 | 736.60 | 714.50 | 689.60 |
| | 8-75065 | 621.00 | 606.50 | 597.70 | 542.90 |
| | 42-6943 | 592.90 | 560.70 | 537.20 | 502.50 |
| 7815 | | 825.80 | 785.60 | 754.40 | 723.60 |
| | 6-75060 | 719.60 | 686.30 | 654.60 | 622.50 |
| | 25-6943 | 666.10 | 642.20 | 624.20 | 611.20 |
| 7836 | | 738.90 | 714.40 | 691.30 | 668.70 |
| | 1-75004 | 643.60 | 626.00 | 609.20 | 593.00 |
| | 25-6943 | 666.10 | 642.20 | 624.20 | 611.20 |
| 7846 | | 803.50 | 772.60 | 744.30 | 709.70 |
| | 21-6937 | 682.60 | 646.80 | 612.00 | 571.10 |
| | 19-6935 | 489.10 | 462.60 | 447.20 | 429.60 |
| 7854 | | 804.50 | 780.40 | 761.60 | 734.00 |
| | 14-6967 | 652.10 | 643.40 | 632.90 | 625.00 |
| | 25-6943 | 666.10 | 642.20 | 624.20 | 611.20 |
| 7856 | | 605.10 | 596.00 | 582.50 | 569.90 |
| | 46-6943 | 564.80 | 541.10 | 528.70 | 501.30 |
| | 3-6969 | 600.20 | 586.60 | 572.60 | 561.50 |
| 7858 | | 453.00 | 432.50 | 418.50 | 398.30 |
| | 9-6957 | 550.30 | 540.30 | 525.80 | 509.50 |
| | 6-75123 | 527.30 | 507.60 | 476.80 | 453.80 |

[z]Each figure represents the average of the two replications.

[y]Upper figure is female parent; lower figure is male parent.

Table 10. *Continued*

| Genotypes | | Harvests | | | |
|---|---|---|---|---|---|
| Progenies | Parents[y] | $H_1$ | $H_2$ | $H_3$ | $H_4$ |
| 7864 | | 429.40 | 409.60 | 380.00 | 353.80 |
| | 9-7410 | 603.70 | 578.00 | 561.20 | 542.20 |
| | 19-6935 | 489.10 | 462.60 | 447.20 | 429.60 |
| 7870 | | 691.10 | 681.40 | 670.00 | 644.90 |
| | 13-75060 | 628.80 | 617.20 | 586.80 | 569.50 |
| | 20-6971 | 670.60 | 654.80 | 637.60 | 622.00 |
| 7873 | | 691.60 | 671.10 | 652.80 | 634.90 |
| | 19-6935 | 489.10 | 462.60 | 447.20 | 429.60 |
| | 3-6969 | 600.20 | 586.60 | 572.60 | 561.50 |
| 7878 | | 726.60 | 704.50 | 680.10 | 671.40 |
| | 16-75056 | 689.90 | 668.40 | 642.70 | 628.00 |
| | 19-6936 | 699.40 | 681.20 | 666.00 | 648.70 |
| 7882 | | 682.00 | 657.60 | 641.80 | 618.50 |
| | 22-6963 | 610.30 | 588.20 | 579.30 | 564.70 |
| | 9-6957 | 550.30 | 540.30 | 525.80 | 509.50 |
| 7886 | | 450.90 | 427.80 | 403.60 | 371.40 |
| | 3-6969 | 600.20 | 586.60 | 572.60 | 561.50 |
| | 22-6963 | 610.30 | 588.20 | 579.30 | 564.70 |
| 7889 | | 712.80 | 682.70 | 660.70 | 641.30 |
| | 16-75081 | 572.30 | 546.90 | 526.70 | 503.80 |
| | 24-75003 | 632.70 | 616.40 | 606.50 | 596.80 |
| 7890 | | 778.50 | 752.90 | 719.80 | 693.50 |
| | 3-75077 | 688.10 | 672.50 | 643.60 | 628.60 |
| | 11-75081 | 681.80 | 666.90 | 639.90 | 608.40 |
| 7899 | | 396.30 | 414.50 | 385.70 | 354.30 |
| | 17-75018 | 698.70 | 681.90 | 658.20 | 629.20 |
| | 1-75092 | 668.00 | 649.50 | 615.90 | 587.80 |
| 78100 | | 715.60 | 692.40 | 662.30 | 630.70 |
| | 1-75092 | 668.00 | 649.50 | 615.90 | 587.80 |
| | 31-75088 | 636.60 | 605.70 | 581.60 | 551.50 |

Table 11. Changes in average capping force (force required for berry detachment in gms) for the progenies and their parental clones in 1981[z]

| Genotypes | | Harvests | | | |
|---|---|---|---|---|---|
| Progenies | Parents[y] | $H_1$ | $H_2$ | $H_3$ | $H_4$ |
| 7801 | | 519.60 | 480.40 | 443.60 | 406.70 |
| | 80-6935 | 695.40 | 659.40 | 634.40 | 597.40 |
| | 6-75123 | 523.80 | 506.90 | 470.10 | 443.60 |
| 7810 | | 756.20 | 738.60 | 719.10 | 689.80 |
| | 8-75065 | 625.90 | 604.60 | 583.90 | 540.20 |
| | 42-6943 | 588.60 | 557.70 | 530.10 | 505.10 |
| 7815 | | 832.60 | 780.70 | 745.60 | 732.70 |
| | 6-75060 | 724.30 | 686.10 | 654.60 | 625.40 |
| | 25-6943 | 663.40 | 646.30 | 629.10 | 612.60 |
| 7836 | | 734.30 | 713.00 | 701.60 | 680.30 |
| | 1-75004 | 641.40 | 619.30 | 607.30 | 584.90 |
| | 25-6943 | 663.40 | 646.30 | 629.10 | 612.60 |
| 7846 | | 805.50 | 778.30 | 749.10 | 709.80 |
| | 21-6937 | 679.60 | 631.70 | 594.80 | 567.20 |
| | 19-6935 | 482.90 | 461.60 | 441.60 | 421.20 |
| 7854 | | 796.10 | 776.50 | 754.00 | 726.20 |
| | 14-6967 | 646.70 | 630.20 | 617.00 | 602.20 |
| | 25-6943 | 663.40 | 646.30 | 629.10 | 612.60 |
| 7856 | | 607.30 | 591.30 | 574.70 | 555.50 |
| | 46-6943 | 568.80 | 544.80 | 523.90 | 494.80 |
| | 3-6969 | 602.10 | 584.10 | 571.80 | 552.40 |
| 7858 | | 458.67 | 441.44 | 424.56 | 408.89 |
| | 9-6957 | 553.80 | 504.60 | 525.40 | 505.60 |
| | 6-75123 | 523.80 | 506.90 | 470.10 | 443.60 |

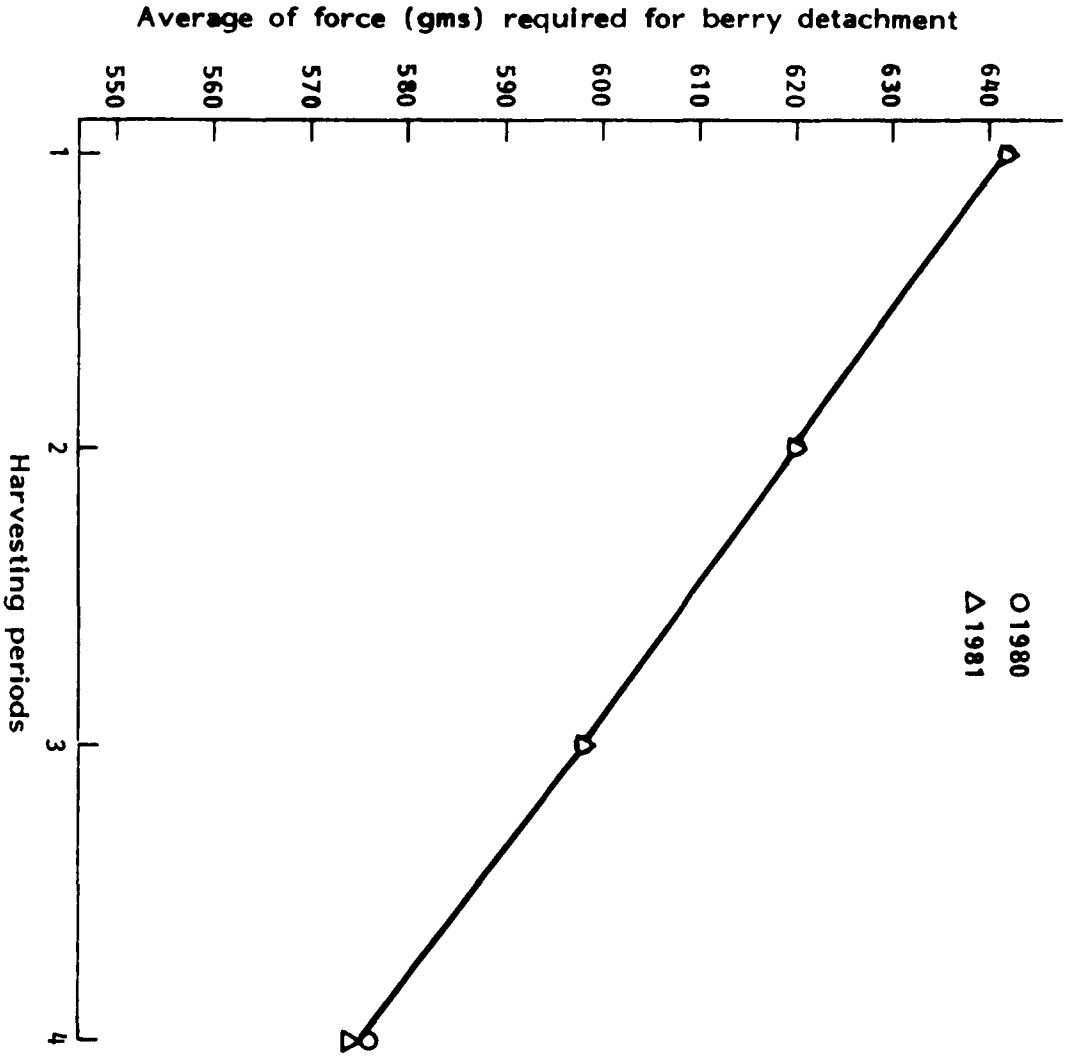
[z]Each figure represents the average of the two replications.

[y]Upper figure is female parent; lower figure is male parent.

Table 11. *Continued*

| Genotypes | | Harvests | | | |
|---|---|---|---|---|---|
| Progenies | Parents[y] | $H_1$ | $H_2$ | $H_3$ | $H_4$ |
| 7864 | | 431.70 | 408.40 | 382.20 | 355.90 |
| | 9-7410 | 592.10 | 580.40 | 567.10 | 543.50 |
| | 19-6935 | 482.90 | 461.60 | 441.60 | 421.20 |
| 7870 | | 686.50 | 671.70 | 660.00 | 644.20 |
| | 13-75060 | 628.50 | 608.90 | 578.20 | 552.90 |
| | 20-6971 | 673.30 | 654.90 | 636.90 | 620.20 |
| 7873 | | 684.30 | 678.50 | 651.60 | 635.20 |
| | 19-6935 | 482.90 | 461.60 | 441.60 | 421.20 |
| | 3-6969 | 602.10 | 584.10 | 571.80 | 552.40 |
| 7878 | | 727.90 | 716.30 | 693.30 | 671.50 |
| | 16-75056 | 688.50 | 668.50 | 633.20 | 606.70 |
| | 19-6936 | 698.30 | 686.70 | 673.70 | 654.90 |
| 7882 | | 683.00 | 661.70 | 642.70 | 625.70 |
| | 22-6963 | 603.40 | 587.00 | 580.60 | 570.50 |
| | 9-6957 | 553.80 | 540.60 | 525.40 | 505.60 |
| 7886 | | 450.20 | 419.60 | 392.40 | 365.20 |
| | 3-6969 | 602.10 | 584.10 | 571.80 | 552.40 |
| | 22-6963 | 603.40 | 587.00 | 580.60 | 570.50 |
| 7889 | | 712.60 | 677.60 | 654.00 | 641.00 |
| | 16-75081 | 573.20 | 541.70 | 524.40 | 503.60 |
| | 24-75003 | 632.80 | 617.00 | 602.50 | 590.10 |
| 7890 | | 776.00 | 750.50 | 718.30 | 691.60 |
| | 3-75077 | 687.90 | 671.40 | 641.90 | 618.90 |
| | 11-75081 | 682.70 | 666.90 | 637.50 | 606.50 |
| 7899 | | 441.10 | 419.80 | 399.30 | 368.60 |
| | 17-75018 | 696.90 | 673.40 | 651.60 | 630.80 |
| | 1-75092 | 668.90 | 644.60 | 611.00 | 586.90 |
| 78100 | | 707.90 | 680.10 | 662.10 | 634.90 |
| | 1-75092 | 668.90 | 644.60 | 611.00 | 586.90 |
| | 31-75088 | 629.20 | 605.90 | 583.00 | 557.20 |

Figure 3. Changes of the average capping force in gms (the force required for berry detachment) during the four harvesting periods for both progenies and parental clones in the 1980 and 1981 growing seasons


Average of force (gms) required for berry detachment
550
560
570
580
590
600
610
620
630
640
1
2
3
4
Harvesting periods
O 1980
Δ 1981

harvesting periods. Also, the statistical analysis using the Tukey test indicated that entity-harvest interaction was significant at .001. Hence, the ranking of the average capping forces during the four harvesting periods in 1980 and 1981 indicates that these averages decreased with the progression of the harvesting periods. Moreover, partitioning the harvest's sum of squares indicated that the relationship between the four harvest times and the average force required for berry detachment appeared to be significantly linear at P = .001 level.

The averages of capping force for all the progenies and their parental clones were ranked in each of the four harvesting periods in 1980 and 1981. In 1980, these averages were 642.19, 620.95, 598.58, and 575.48 gms; likewise, in 1981, the averages were 642.45, 619.76, 597.22, and 573.70 gms for the first, second, third, and fourth harvesting periods, respectively.

## Relationships of the Characters during the Four Harvesting Periods

### Yield and concentrated ripening traits

Regression and correlation were estimated for determining the relationships between the number of berries per plant and the percentage of ripe berries during the four harvesting periods. Multiple regression was constructed to test for significant effect of yield on the concentrated ripening for each harvest date. Statistical analysis showed that high concentrated ripening contributed to higher yielding ability. The explained variation in yield by a quadratic function of concentrated ripening was 0.743, 0.613, 0.606, and 0.666 for the first, second, third, and

fourth harvests, respectively, in 1980. These explained variances in 1981 were 0.859, 0.744, 0.841, and 0.797. In 1980 and 1981, the regression of these traits to each other through the four harvesting periods for all genotypes studied is illustrated in Figures 4, 5, 6, and 7.

It was found that most of the progenies and their parental clones tended to concentrate their fruit ripening through the second and third harvesting periods. At these two harvests, however, most of the genotypes produced the highest average number of berries per plant as compared to the first and fourth harvesting times.

For both the 1980 and 1981 growing seasons, most of the genotypes ripened about 5 to 14 percent of their berries during the first harvesting period. However, 17 to 25 percent of the berries were ripened by a very few genotypes in both years, as shown in Figure 4.

During the second harvest, 36 to 46 percent of the berries were ripened by most of the progenies and the parental clones in 1980, as compared to 39 to 48 percent in 1981. A very few genotypes, however, ripened 24 to 34 and 27 to 37 percent of their berries in 1980 and 1981, respectively, as illustrated in Figure 5. Also, in the third harvesting period, most of the genotypes produced high percentages of ripe berries. These percentages ranged from 36 to 44 in 1980 and from 34 to 44 in 1981. In contrast, certain genotypes ripened about 25 to 35.8 percent and 24 to 36 percent of their berries in 1980 and 1981, respectively (Figure 6).

The last harvest indicated that the percentages of berries ripened by most of the progenies and their parental clones ranged from 6 to 14 percent and from 5 to 13 percent for 1980 and 1981 growing seasons,

Figure 4. Relationship between yield (average number of berries per plant) and concentrated ripening (percent of mature or ripe berries) for the progenies and their parental clones in 1980 and 1981 at the first harvest

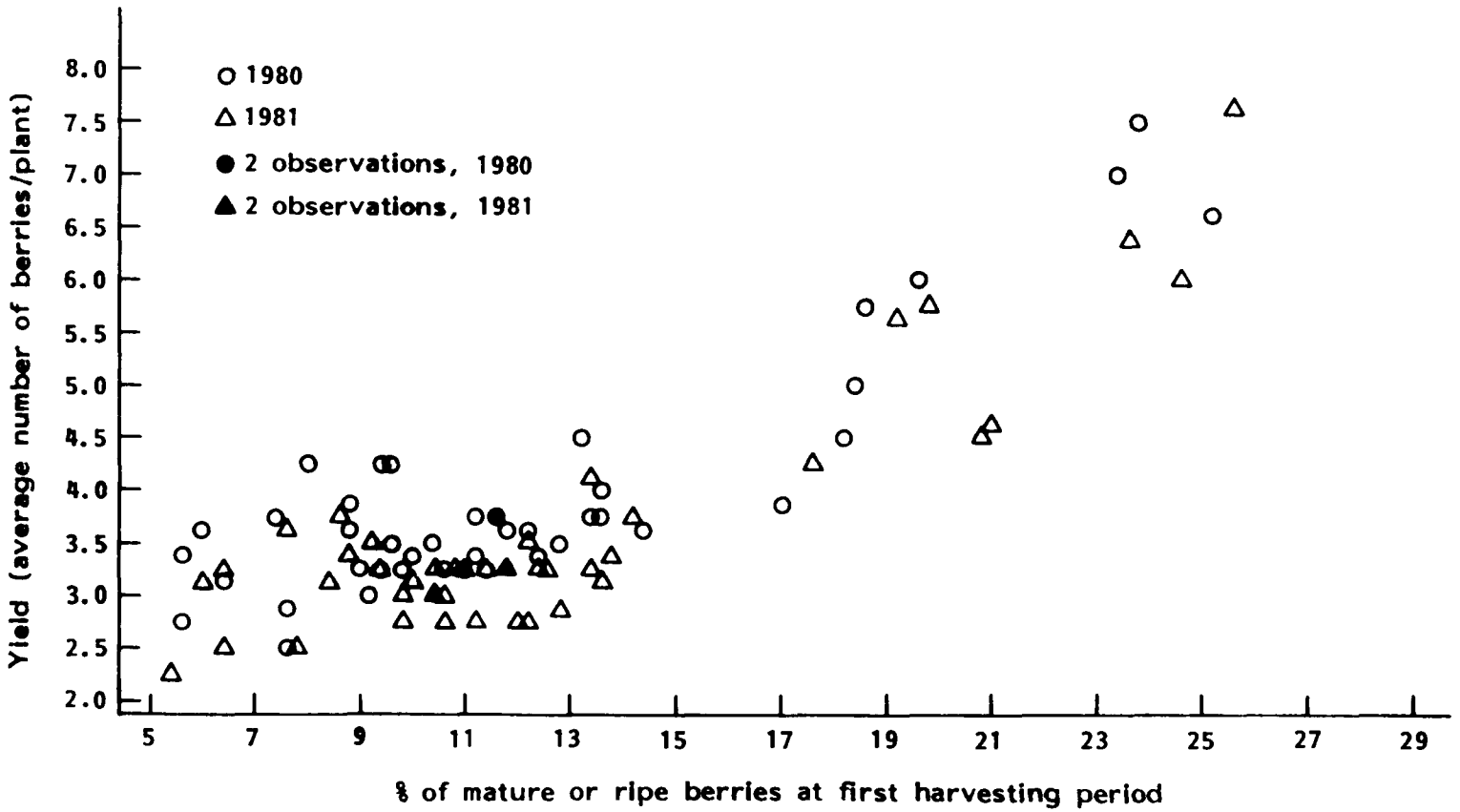

Yield (average number of berries/plant)
8.0
7.5
7.0
6.5
6.0
5.5
5.0
4.5
4.0
3.5
3.0
2.5
2.0
○ 1980
△ 1981
● 2 observations, 1980
▲ 2 observations, 1981
5
7
9
11
13
15
17
19
21
23
25
27
29
% of mature or ripe berries at first harvesting period

Figure 5. Relationship between yield (average number of berries per plant) and concentrated ripening (percent of mature or ripe berries) for the progenies and their parental clones in 1980 and 1981 at the second harvest

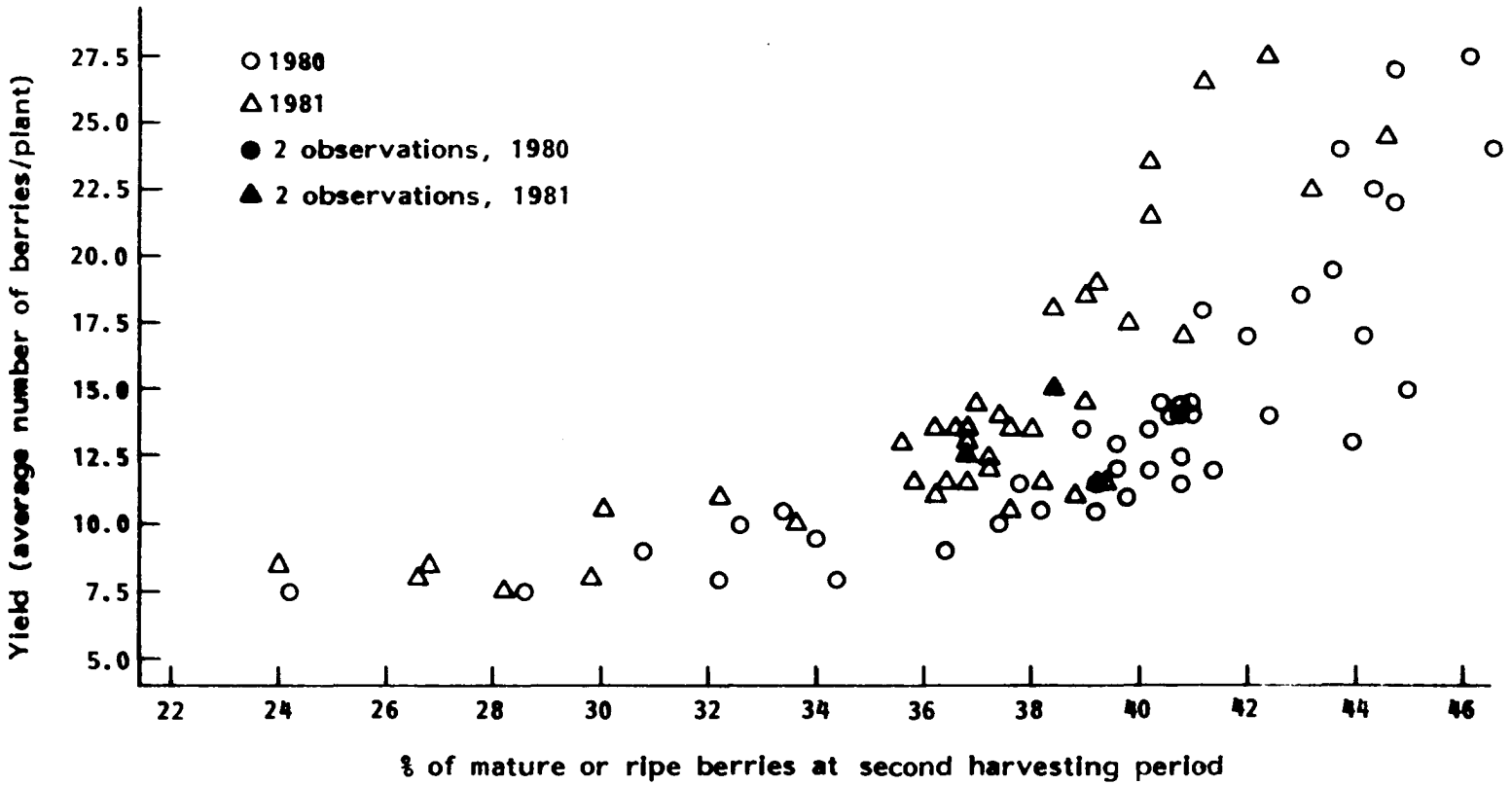

○ 1980
△ 1981
● 2 observations, 1980
▲ 2 observations, 1981
Yield (average number of berries/plant)
27.5
25.0
22.5
20.0
17.5
15.0
12.5
10.0
7.5
5.0
22
24
26
28
30
32
34
36
38
40
42
44
46
% of mature or ripe berries at second harvesting period

Figure 6. Relationship between yield (average number of berries per plant) and concentrated ripening (percent of mature or ripe berries) for the progenies and their parental clones in 1980 and 1981 at the third harvest

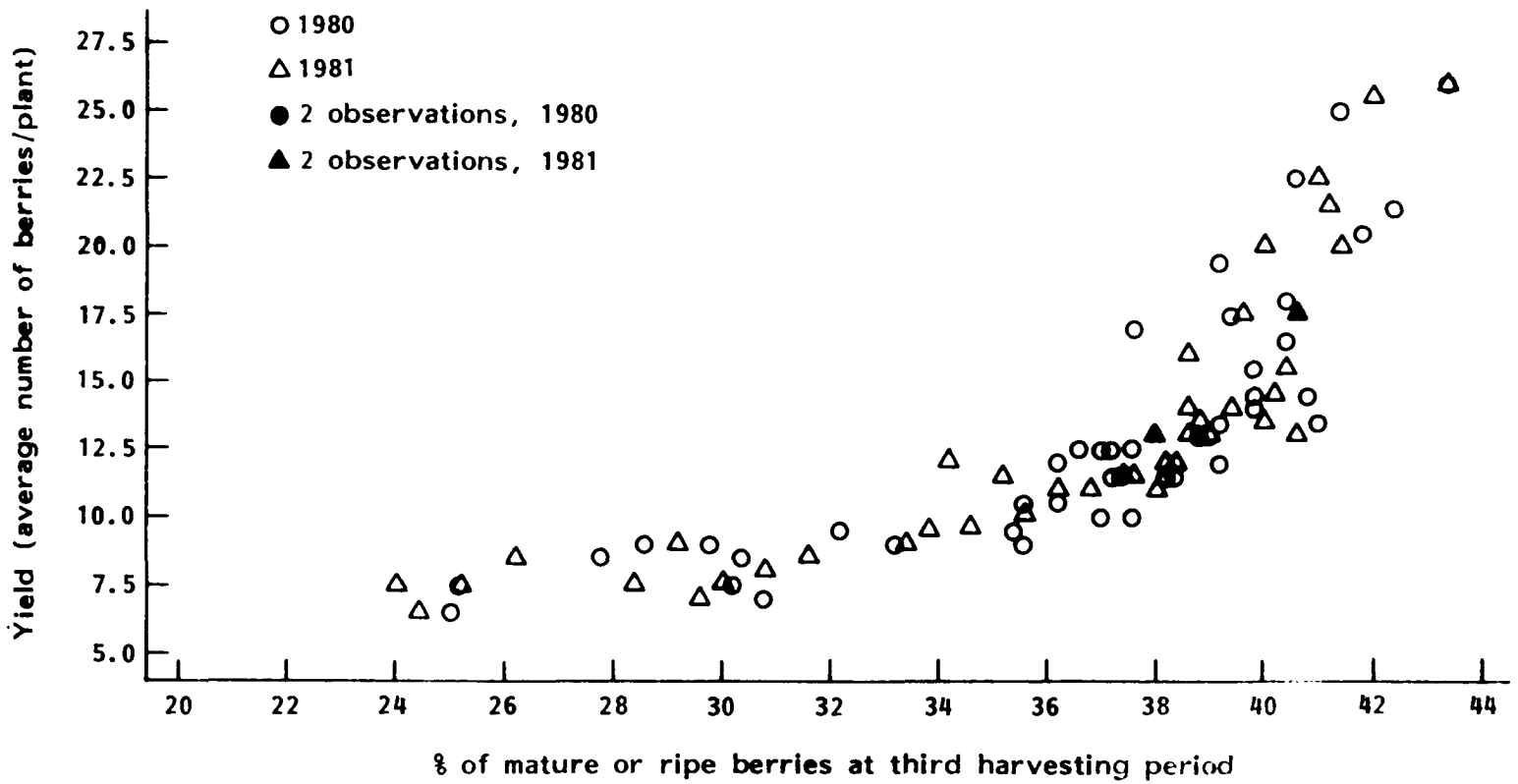
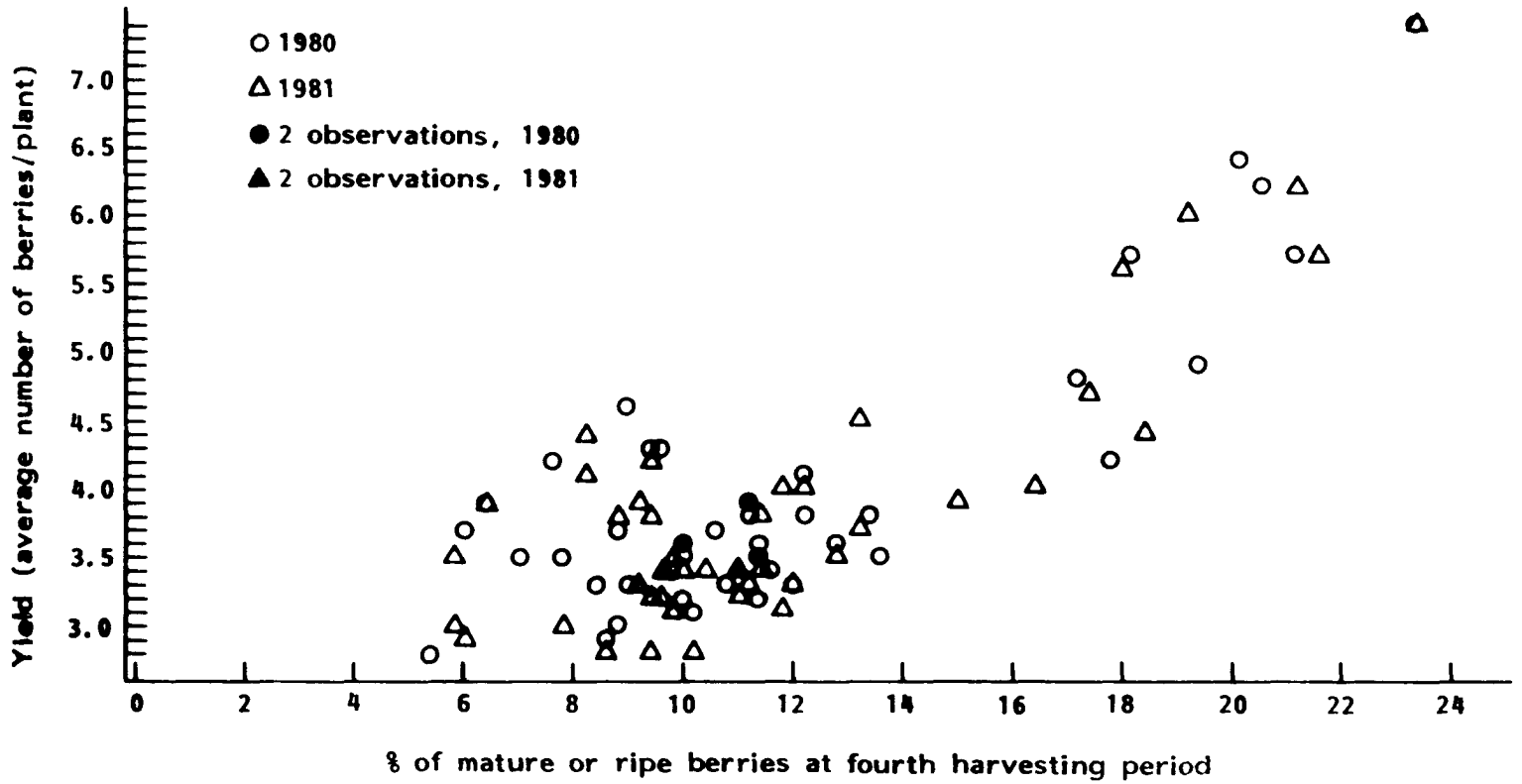

○ 1980
△ 1981
● 2 observations, 1980
▲ 2 observations, 1981
Yield (average number of berries/plant)
27.5
25.0
22.5
20.0
17.5
15.0
12.5
10.0
7.5
5.0
20
22
24
26
28
30
32
34
36
38
40
42
44
% of mature or ripe berries at third harvesting period

Figure 7. Relationship between yield (average number of berries per plant) and concentrated ripening (percent of mature or ripe berries) for the progenies and their parental clones in 1980 and 1981 at the fourth harvest


○ 1980
△ 1981
● 2 observations, 1980
▲ 2 observations, 1981
Yield (average number of berries/plant)
7.0
6.5
6.0
5.5
5.0
4.5
4.0
3.5
3.0
0
2
4
6
8
10
12
14
16
18
20
22
24
% of mature or ripe berries at fourth harvesting period

respectively. However, a few progenies produced about 17 to 24 percent and 15 to 23 percent ripe berries during this period in 1980 and 1981, respectively (Figure 7).

Moreover, a strong relationship between yield and concentrated ripening traits was detected by estimating the correlation coefficient values. The statistical analysis indicated that there was a strong positive correlation between these traits in both 1980 and 1981. The correlation values were $r = 0.898$ for 1980 and $r = 0.892$ for 1981.

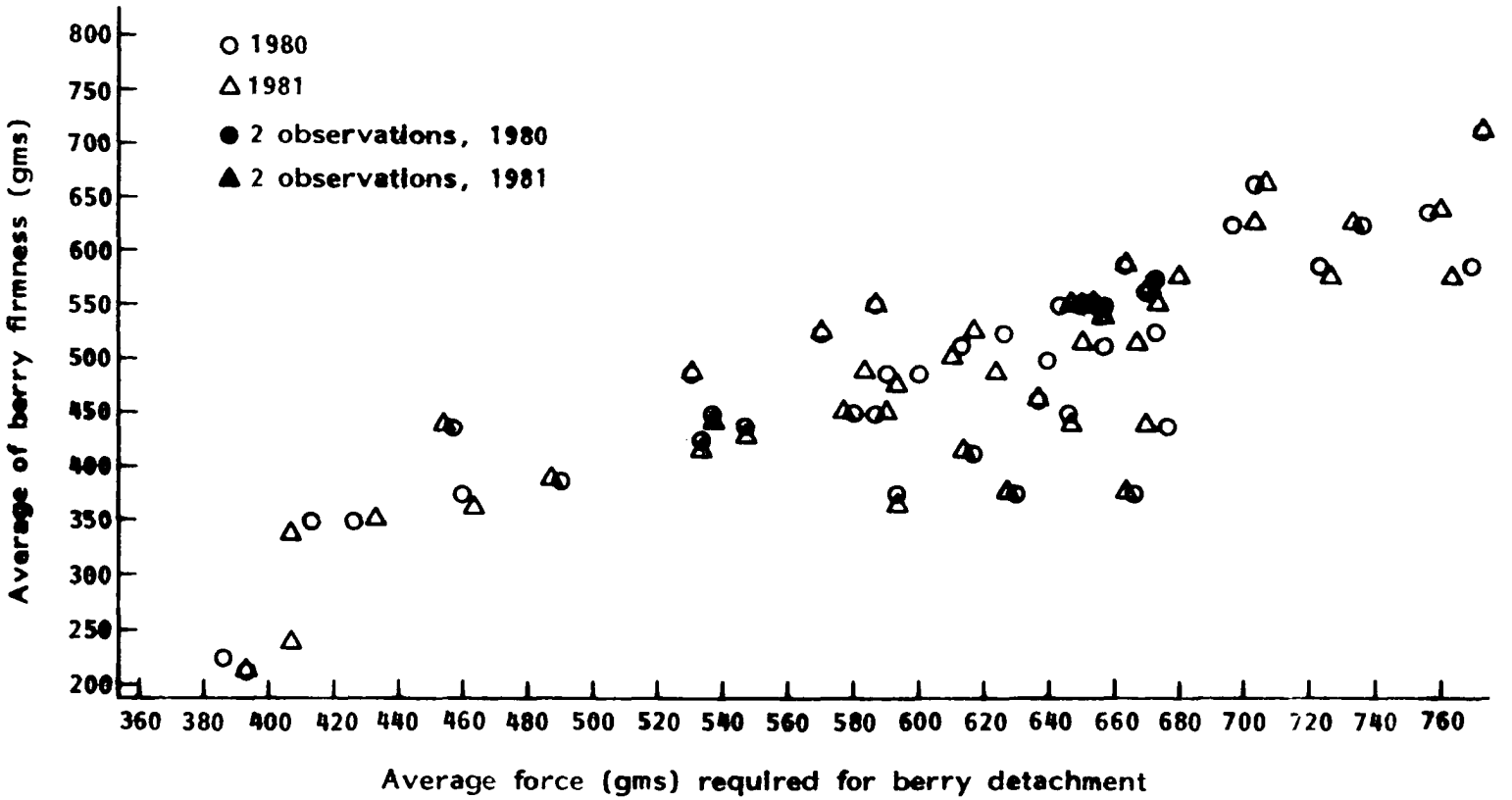
Firmness and easy cap traits

For determining the relationship between the average of berry firmness (gms) and the easy cap (average force required for berry detachment in gms) traits, regression as well as correlation were estimated. Simple linear regression was constructed to test for significant effect of berry firmness on the force required for berry detachment. Statistical analysis indicated that firmer fruits required greater force for detachment from the plant. The explained variation in firmness by a simple linear relationship to capping force was 0.690 in 1980 and 0.689 in 1981. The regression of the average berry firmness to the easy cap trait is illustrated in Figure 8 for both the progenies and their parental clones in the 1980 and 1981 growing seasons. Strong relationship was found between the two characters. It was found the genotypes that tended to produce firm fruits required higher force for berry detachment and vice versa.

Moreover, correlation coefficient values were estimated in 1980 and 1981 which strongly support this relationship. The statistical analysis of the data in 1980 and 1981 indicated that the correlation between the

two characters was strong and positive. The correlation values were $r = 0.846$ and $r = 0.845$ for 1980 and 1981, respectively.

Figure 8. Relationship between berry firmness (gms) and easy cap (gms) characters for the progenies and their parental clones in 1980 and 1981


○ 1980
△ 1981
● 2 observations, 1980
▲ 2 observations, 1981
Average of berry firmness (gms)
800
750
700
650
600
550
500
450
400
350
300
250
200
360 380 400 420 440 460 480 500 520 540 560 580 600 620 640 660 680 700 720 740 760
Average force (gms) required for berry detachment

# DISCUSSION

The results of this study indicated that crosses between certain strawberry selections improved, to some extent, the berry characters that related to mechanical harvest. This improvement is expected to promote mechanical harvesting and help stabilize the strawberry industry (29).

In both 1980 and 1981 growing seasons, tremendous variations for the average number of berries per plant were found in all genotypes studied. However, most of the progenies showed higher significant differences than their own parental clones, and in this matter they were superior. Heterosis, the most satisfactory explanation that may be applied to this case, refers to the phenotypic expression of a character in the hybrid when it has a value beyond the parental limits (7). Øydvin (77) found the number of berries per plant was as large in the $F_1$-average as in the parent-average. Significant correlations were found between parent cultivars and progenies with regard to the number of berries per plant.

Wenzel et al. (96) reported that significant differences were obtained between cultivar means for yield and number of berries per plant. Great proportion of the total variation among cultivars with regard to these traits was due to genetic effects. He, therefore, suggested that selection among cultivars followed by vegetative propagation will be highly effective. Genetic progress should then be highest by selection among progenies to be followed by selection among seedlings of the superior progenies. Moore and Brown (60) found marked differences in total yields existed among selections.

Consideration of total yields is important in evaluation of once-over harvest potential, since the amount of usable fruit that can be harvested

at any one time is determined by the percentage of fruit ripe and the total productivity of the cultivar. Regarding breeding for concentration ripening, Denisen et al. (31) reported that this characteristic is transmitted from one generation to the next by genetic principles. The results of the present study agreed with those reported by them. It was found that, for most of the progenies, when both parents were highly concentrated types, their progeny was more highly concentrated than that resulting from one concentrated and one nonconcentrated parental type.

It was noticed that almost all genotypes studied tended to ripen high percentages of their berries during the second and third harvesting periods as compared to those percentages during the first and fourth harvests in both the 1980 and 1981 growing seasons. As a consequence, there were significant differences between the four harvesting periods with regard to the percentage of ripe berries for each period. The relationship between the four harvesting periods and the percentages of ripe berries appeared to be quadratic. This result strongly supports the changes of the percentages of ripe berries throughout the four harvest times. These results were in complete agreement with those reported by Guttridge and Anderson (36), who stated that the second and third mown harvests yielded considerably more marketable fruit than the first one. Moore and Brown (60) reported most of the cultivars that were harvested at weekly intervals, for 3 weeks, reached a peak period of maturity during the second week of harvest.

Denisen et al. (32) noted that concentrated ripening types do not follow the traditional primary, secondary, tertiary, etc. sequence in ripening, but tend to "bunch" them together. This phenomenon usually occurs as a result of aborted blossoms. In some instances, the primary berry does

not develop, the secondary and tertiary berries develop almost simultaneously, and the quartenary and quintary blossoms tend to abort. Thus, it is not uncommon for an entire cluster of strawberries to be ripe at one time. Concentrated ripening selections were characterized by higher percentages of ripe and partially ripe secondary and tertiary fruit and high abortion rate and/or arrested development in late-blooming flowers (89). Many progenies during 1980 and 1981 gave higher percentages of ripe berries during the second and third harvesting periods. Some of them reached up to 89%, which makes them more promising for the future of mechanical harvesting of strawberries. Denisen and Buchele (30) considered that cultivars which had over 50% of their crop ripe and harvestable at one time were candidates for machine harvesting.

Regarding the relationship between yield and concentrated ripening traits, it was found that most of the progenies and their parental clones tended to concentrate their fruit ripening through the second and third harvesting periods. At these two harvests, however, most of the genotypes produced the highest average number of berries per plant in comparison to the first and fourth harvesting times. Moreover, a strong relationship between yield and concentrated ripening traits was detected by estimating the correlation coefficient values. The statistical analysis indicated there was a strong positive correlation between these traits in both 1980 and 1981. Also, the statistical analysis indicated that high concentrated ripening contributed to higher yielding ability. The indication of that was that the higher yielding genotypes had the more concentrated ripening ability, as compared to the lower yielding ones. These results were confirmed by those obtained by Guttridge and Anderson (36), who concluded

that higher-yielding cultivars had the more concentrated ripening periods, as measured by percentages of marketable fruit harvested at a single picking. They found the overall mean proportions of marketable fruit as percentages of hand-picked fruit increased from 25% for the first harvest to 38% and 40% for the second and third harvests.

Moore et al. (63) reported that the combination of high seasonal yield and high percent concentration of ripening would result in the greatest single harvest yield. The relationship between these factors is inconsistent and varies among seasons and locations. However, these factors are independent traits, and it appears possible to combine them in a single clone. They concluded that development of a clone with the concentrated ripening and high seasonal yield traits would result in a very good once-over yield and greatly enhance the feasibility of mechanical harvest of strawberries. Thus, selection in breeding programs should be for both concentration of maturity and high total productivity (60).

It was clear from the results of the present study that there was a positive correlation between the yield and percent of ripe berries at a given harvest. High weekly yield positively correlated with high weekly percent ripening concentration was found in 1 of 9 comparisons by Moore et al. (63).

Satisfactory handling quality depends upon firm flesh and tough epidermis of the fruit (82). A firm flesh and tough skin are 2 important characteristics which strawberry breeders strive to incorporate into new cultivars. The susceptibility of a strawberry fruit to damage upon removal from the plant is not only of concern to the breeder, but to the retailer who is interested in an attractive fruit with a long shelf-life

and to the engineer involved in the design of machinery for mechanical harvesting (75). Denisen et al. (31) reported that a major objective of the breeding programs for strawberries adapted to mechanical harvest is the development of selections with very firm flesh and tough skins to withstand harvester abuse.

The results of this study indicated that the average firmness of the berries varied greatly for the progenies and their parental clones in 1980 and 1981. In both seasons, it was noticed the ranges of the average berry firmness for parents fell within the ranges of their offspring, which indicated that certain progenies were superior and others were inferior to their parental clones. Moreover, the differences between the genotypes were highly significant, statistically. However, the present study differs from that of Scott (81), who reported that rating for firmness of fruit indicated there were no differences occurring among the seedlings. Also, there were no significant correlations between fruit size and the ratings for firmness of fruit. He also pointed out that seedlings derived from *F. virginiana* x cultivated cultivars were very soft-fruited, but differences in progenies were noted as being related to the firmness of the cultivated parents. Hondelmann (41) reported the heritability of fruit-firmness is considerable. Wide variations in firmness occurred among fruits within samples and within individual fruits (23).

The data obtained during this study revealed, to some extent, that the superiority or the inferiority of the progenies with regard to this trait was dependent upon the performance of their parental clones. This trait did follow the same principles that were detected in concentrated ripening character through its transmission from the parental clones to their

progenies. It was found that if the two parents have high averages of berry firmness, their progeny, always, has as high or higher average of berry firmness than its parental limits. Although the parental clones of the progenies 7801, 7858, 7864, 7886, and 7899 had reasonable averages of berry firmness, these progenies were lower than their parents in 1980 and 1981 growing seasons. The genetic segregations of the genes that control berry firmness may be the possible explanation for this situation.

The results also indicated that the average of berry firmness greatly varied from one harvest to the other. This average decreased with the progression of the harvesting times. The ranking of the average berry firmness during the four harvesting periods in 1980 and 1981 indicated that berry firmness decreased from the first through the fourth harvests. The possible interpretation of this is that full and 3/4 colored berries were picked at each harvesting time, whereas all berries that were 1/2 or less colored were left for the next harvest. Three-day intervals between each two harvests may be so long that most of the 1/2 or less colored berries would be overripe, and, as a consequence, the berry firmness dropped from one harvest to the next, and so on. Statistical analysis revealed that the relationship between the four harvests and the average of berry firmness appears to be linearly significant.

Cap removal from strawberries has long been an important problem from the standpoint of labor costs (59). The easy cap trait (removing the berries with the calyx remaining attached to the plant) was determined as the force required for berry detachment. In comparing the progenies and their parental clones, the results obtained in 1980 and 1981 seasons indicated

that the average force required for berry detachment was varied among the progenies, among the parents, and between the progenies and their parental clones. These results were supported by those found by Brown and Moore (20), who reported that certain cultivars differed significantly in the force required for capping. Also, Brown and Moore (19) reported that progenies from *F.* x *ananassa* x *F. virginiana* crosses required significantly less force to cap than progenies derived wholly from *F.* x *ananassa*. Also, the progeny means varied significantly for capping percentage and for capping and pedicel breaking force.

The work of Barritt (9) indicated that wide variation in the capping ease trait was found among 27 parental clones. Three aspects of his study support the contention that a high proportion of genetic variance for capping ease is additive: 1) the high estimate of heritability, 2) the much larger GCA (general combining ability) mean square than SCA (specific combining ability) mean square in the analysis of variance of progeny data, and 3) a significant correlation of phenotypic parent ratings with genotypic GCA parent values.

The results of the present study indicated that the ranges of the average force required for berry detachment for the parental clones fell within the ranges of their progenies. The indication was that certain progenies were superior, whereas some others were inferior to their parental clones. Also, it was noticed that the differences between all genotypes studied were statistically highly significant. Moreover, it was found that parental clones requiring high capping force produced progenies equal to or higher than their parentage limits. Lawrence and Martin (54) found that when both parents were easy cap types, seedling rating exceeded either

parent. As might be expected, the percentage of easy cap types in the progeny from such crosses was greater than from crosses to easy cap by difficult-to-cap parents.

From the results obtained in 1980 and 1981 with regard to the easy cap trait, it was found that selection of the parental clones on the basis of their performance and their phenotypes might be the most effective way for concentration of this character through few generations of crosses between superior phenotypes. However, the present study differed from that of Brown and Moore (19), who found that capping force was influenced by environment, and had low heritability. As a consequence, they concluded that parent phenotypes could not be used to predict progeny performance, but the general combining ability scores were useful for identifying promising parents. Also, they reported that since the cultivars were heterozygous and the characters were controlled by many genes, mating the best phenotypes will not always result in the most rapid breeding progress. In contrast, because considerable additive genetic variance exists for capping ease, Barritt (9) suggested that selecting parents on the basis of their phenotypes would produce predictable genetic gains in offspring performance.

In addition, the results of the present study indicated that the average of the force required for berry detachment decreased from the first through the fourth harvesting periods for all the genotypes studied. The statistical analysis indicated that the averages of capping force were greatly different between the four harvests. The ranking of the average capping forces during the four harvesting times in 1980 and 1981 showed that these averages truly decreased with the progression of the harvests.

The relationship between the four harvesting periods and average force required for berry detachment appeared to be significantly linear as indicated by the statistical analysis.

Strong relationship was found between the capping force, or easy cap, and berry firmness traits. It was found the genotypes that tended to produce firm fruits required higher force for berry detachment and vice versa. Moreover, correlation coefficient values were estimated in 1980 and 1981 which strongly support this relationship. Also, the statistical analysis in 1980 and 1981 indicated that the correlation between these two characters was strong and positive. There seems to be evidence that the genes which control these two traits are strongly linked. The difficulties are that for the breeding programs, this linkage will be an obstacle for developing clones which have firm fruit, and at the same time require less force for berry detachment. Both traits are very important for developing cultivars adapted to mechanical harvesting of strawberries. Lawrence and Martin (54) reported that the highest percentage of easy cap types had soft fruit. This softness is a serious problem in breeding, because firm fruit with resilient skin is needed for machine handling.

# SUMMARY AND CONCLUSIONS

There seems to be definite evidence that the breeding method which has been used, during this study, to any extent for the improvement of this crop was considered the most effective one. This method consisted essentially of crossing chosen clones and selecting a desired superior type from the resulting progeny. However, as the available clones become very highly selected, further improvement becomes progressively more difficult. Larger populations of parental clones are necessary to provide a better chance of selecting a progeny better than those already available. Moreover, a particular progeny could be superior to its own parental clones in some particular trait and may be inferior in some other important ones.

Sexual propagation is always followed by gene segregations; therefore, production of some superior and some inferior progenies could be expected. Hence, mating the selected parental clones is followed by selection among their progenies, then selection from seedlings within the superior progenies may be the most effective method for breeding for one or more traits.

In certain progenies, mating of selected clones increased the average number of berries per plant as compared to the mean averages for both parents. However, some other progenies showed no differences, or lower average number of berries per plant, than their own parental clones. Also, the average number of berries, as well as the percentage of ripe berries, changed from one harvest date to another. Quadratic relationship between percentages of ripe berries and the four harvests was detected in both 1980 and 1981. The percentages of ripe berries reached a peak during the second and third harvests for most of the genotypes studied in 1980 and 1981.

Regression and correlation used in this study indicated that there was a strong relationship between yield and concentrated ripening traits. It was found that the high yielding genotypes usually concentrated high percentages of their berry ripening within a short period of time. The transmission of concentrated ripening trait depends upon the performance of the parental clones. If these two parents were highly concentrated ripening, usually their progeny was highly concentrated too, rather than for one high and one low concentrated ripening parents. Many progenies in 1980 and 1981 concentrated their berry ripening through second and third harvest dates. Some progenies ripen about 89% of their berries during these two harvests, which is considered more promising for the future of mechanical harvesting.

The average berry firmness was affected by the crosses between the parental clones in 1980 and 1981 growing seasons. It was found, in many cases, that the average berry firmness for the progeny exceeded the mean averages of both parents. These progenies are considered as candidates for mechanical harvest. In contrast, some other matings decreased the berry firmness, or showed no differences between the progeny and its parental clones.

The average of berry firmness, however, changed with the progression of the four harvesting periods; it was decreased with the harvests. Linear relationship was observed between the average of berry firmness and the four harvesting times.

Easy cap trait (the average force required for berry detachment) also was affected by the parental matings. In 1980 and 1981, the results of the present study indicated that some progenies had higher averages of

force required for berry detachment than the mean averages of its own parental clones and, consequently, these progenies are considered as non-easy-cap, whereas some other progenies had averages of force required for berry detachment less than that obtained by their parental clones, and they are considered easy-cap types.

The capping force was changed with the progression of the harvest dates for most of the genotypes studied in 1980 and 1981. It decreased from one harvest date to the next. The relationship between the capping force and the four harvesting periods was linear.

Finally, regression and correlation used in the present study detected a strong relationship between berry firmness and easy-cap traits. It was found that the easy-cap types which required less force for berry detachment usually had soft berries and vice versa. The genes which govern these traits seem to be linked together. The disadvantages of this for breeding programs are the difficulties to breed for both traits in one clone. As known, the breeding for firm fruits and easy cap removal are the most important objectives for the mechanical harvesting of strawberries. According to the results obtained during this study, breeding for one character at a time may be the most expedient way.

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# PART II.

# CYTOGENETICAL STUDIES OF PARENT AND PROGENY

# INTRODUCTION

The modern cultivated strawberry *Fragaria* x *ananassa* Duch. is octoploid with 2n = 56, and is believed to have originated as a hybrid between the two American octoploid species, *F. virginiana* Duch. and *F. chiloensis* (L.) Duch. (6, 7, 9, 23). A large pool of genetic variability is present in these species which makes it possible to improve the plant and fruit characteristics. Although cytogenetical studies in different *Fragaria* species have been initiated by several workers in the 1920s, little is known about the inheritance of qualitative and quantitative traits. These difficulties may be due to the genetic complexity and the high heterozygosity of the octoploid cultivars.

Because of the small size of the chromosomes which ranged between 0.5μ to 1.5μ (38), the high somatic number of the chromosomes, and the lack of genetic markers in the octoploid cultivar, it was difficult to identify individual pairs of chromosomes and to prepare a Karyotype of the strawberry. However, many attempts have been made to investigate the cytological behavior of the chromosomes and the type of chromosome pairing during meiosis. The information regarding chromosome pairing is of great importance for any phenotypic segregation must be interpreted according to the pairing and disjunction of the chromosomes during meiosis. Chromosome pairing is also of importance in understanding how the genetic material in such highly polyploid species is organized and distributed during meiotic division (5).

Through the study of the chromosomal behavior during meiosis of *Fragaria* polyploids, secondary association between bivalents has attracted the

attention of several investigators for assessing the relationships between the different genomes. However, the assessment of genome homology based on chromosome pairing is difficult and subjective (27). Sebastiampillai and Jones (35) wrote:

> Cytogenetical studies in *Fragaria* polyploids have been made by several workers with a view to assessing phylogenetic relationships. But interpretations and conclusions of these workers with regard to the nature of polyploids are not always in agreement.

Studies of meiosis in octoploid *F.* x *ananassa* indicated that chromosomes behave normally and tend to pair as bivalents (5, 14, 15, 24, 30). However, association between bivalents has been observed during diakinesis in different *Fragaria* species (26, 34, 35, 42).

The objectives of these studies were to compare the variation in the chromosomal association during meiosis between the progenies and their parental clones and to investigate the nature of any association between the bivalents during diakinesis and metaphase I. A second objective was to investigate mitosis in root tip cells of all genotypes studied to determine whether specific chromosomes could be identified.

# LITERATURE REVIEW

In studying the meiosis of hybrids resulting from intergeneric crosses between *Fragaria* and *Potentilla*, Asker (1) concluded that chromosome configuration in metaphase I indicated that very little pairing occurs between the chromosomes from the two genera. He attributed the high frequency of bivalents as well as trivalents in the *F. moschata* x *P. fruticosa* hybrid to the probable pairing between homologous chromosomes from the three *Fragaria* genomes. Bhanthumnavin (2) provided evidence that the three basic chromosome sets of the hexaploid *F. moschata* are homologous. However, the chromosome association which is highly regular with bivalent formation indicated there may be some factors which restrict the formation of multivalents in this species. He also recognized the possibility of variation between autotetraploid individual seedlings within a species when he emphasized the limitations of comparing mean quadrivalent frequencies in individual autotetraploid plants of *F. vesca*, *F. nubicola*, *F. viridis*, and *F. nilgerrensis*.

Cytological diploidization in the cultivated octoploid strawberry *Fragaria* x *ananassa* was studied by Byrne and Jelenkovic (5); in all cultivated genotypes, all of the chromosomes were associated as bivalents during meiosis. A small proportion of the complement in a few of the pollen mother cells was scored as quadrivalents. The configurations that were scored as such were not the expected configurations, but rather end-to-end or side-to-side associations; thus, they stated these configurations were probably pseudomultivalents and not genuine multivalents. They concluded that meiotic chromosomes in this species are paired exclusively as

bivalents. The reason for the absence of multivalents in normal octoploid *F. ananassa*, in spite of the apparent existing homoeology among its genomes, is not clear. One explanation that may be offered is preferential pairing, i.e., only homologous chromosomes pair (A with A, A' with A', B with B), whereas homoeologous chromosomes never pair (A with A', A with B, A' with B). If such a controlling system was operating, at least occasional multivalents would be expected. This would be particularly true for chromosomes of the B genome present in two sets.

The occurrence of trivalents as well as quadrivalents in the diakinesis of $F_1$ derived from crosses between the diploid *Fragaria vesca* and the octoploid *F. grandiflora* led Dogadkina (8) to state that homology between the genome of *F. vesca* and one genome of *F. grandiflora* was present in addition to the occurrence of autosyndesis between two other genomes of the octoploid. He hypothesized that variable behavior of homologous genomes is probably due to some extrinsic factors. He supported his hypothesis by the fact that all the diploid species involved in the crosses were easily crossed with each other and produced fertile or partly fertile hybrids, all octoploid species were cross-compatible and produced fertile hybrids, and the diploid x octoploid cross, viz. *F. vesca* x *F. virginiana*, yielded very different results with different investigators. He concluded that polyploid species of *Fragaria* consist of very similar genomes, and the diploid species that are very closely related contributed to their formation. On the same point, Ellis (10) demonstrated that three of the four pairs of sets in the octoploid species may be cytologically distinct, but all the polyploid species appear to have at least one common genome.

The genome analysis of the genus *Fragaria* by Fadeeva (11) revealed that successful hybrids resulting from crosses between the hexaploid garden strawberry *F. moschata* and *F. ananassa* were due to some homology between their genomes. The meiotic study of these hybrids with 2n = 49 indicated that the three genomes of *F. moschata* were homologous to the three genomes of *F. ananassa*. He found a strong genetic similarity among the genomes of the genus of the strawberry, homoeology, and for many species, homology. He considered that the fertility of the hybrids resulted from the homology of the genomes in crosses between the different species.

Earlier works of Fedorova (12, 13) indicated that all octoploid strawberry species have the same genomic constitution, AABBBBCC. The observations of the survey made by Gupta (14) indicated that diploid, tetraploid, and octoploid strawberry strains have quite normal chromosome pairing with regular meiotic division. Seven, 14 and 28 bivalents were observed at diakinesis for the diploid, tetraploid, and octoploid, respectively. However, the meiotic studies of the heptaploid strains revealed the presence of univalents and bivalents at diakinesis. The distribution of the chromosomes at anaphase I was found to be irregular.

Ichijima (15) cytologically investigated two American types of the strawberry species, *Fragaria virginiana* and *F. glauca*, and found that both possessed 28 chromosomes as the gametic number. He concluded that counts could best be made in late diakinesis. His observations indicated the behavior of the chromosomes is quite regular.

Jones (17) found that chromosome pairing in a number of diploid interspecific hybrids of strawberry was more or less as regular as that in parental diploid species. Although all the chromosome sets are homologous,

many of these hybrids were partly and some were completely sterile. This sterility indicated that there may be small cytological differences between the species, differences that do not affect chromosome pairing, but which lead to irregular genetic complements in the gametes. He found some cytological evidence that the chromosome sets of some diploid species are not identical. He assumed that all the chromosome sets in the polyploid species are likely to be similar cytologically, i.e., are at least partly homologous, although there may be some genetic differences. During meiosis, a number of associations of four chromosomes may be found, indicating at least four of the sets are homologous or partly so. He stated that the frequency of these associations is lower than would be expected, but a comparison with chromosome pairing in induced autopolyploids, in which all the chromosome sets are known to be homologous, indicated that this low frequency does not necessarily indicate a lack of homology. Also, chromosome pairing in the hybrids between polyploid and diploid species confirmed that at least one set in the polyploids is homologous with that of the diploid species.

Longley (24) generalized that octoploid *Fragaria* species and cultivars have a haploid chromosome number of 28. He found that all chromosomes paired at diakinesis, the normal manner in which the metaphase plate is formed. This regular behavior seemed to be the rule in this octoploid group of *Fragaria*, whether the form came from wild species or highly specialized garden cultivars. However, a few exceptions to the regular meiosis that characterized octoploid *Fragaria* occurred in $F_1$ plants of crosses *F. chiloensis* x *F. virginiana*. Exceptions included univalent chromosomes at diakinesis, and in rare cases, at metaphase plate. More common was the

condition in which both univalent and bivalent chromosomes were present and the distribution of chromosomes to the daughter nuclei was irregular.

Nine octoploid strawberry cultivars were cytologically examined at the diakinesis stage by Mok and Evans (26). Generally, they found the chromosome pairing at diakinesis to be similar in all cultivars. Multivalents were found in all of the nine cultivars; quadrivalents and hexavalents occurred frequently, but few octovalents were observed. The frequency of the number of chromosomes associated as multivalents per cell did not differ significantly between most of the cultivars. They found some differences in pairing among bivalents; the chromosomes were paired closely in most cases, but in a few cases the chromosomes were only loosely associated. They were not sure whether the loose association was due to the stage of meiosis or to the degree of homology between the chromosomes. Another deviation from normal diakinesis was the number of bivalents at the periphery of the nucleolus. They concluded that multivalent formation indicated the existence of homologies between genomes of the cultivated strawberry. In spite of these kinds of irregularities, they observed that the post-diakinesis stages in *F. ananassa* were normal. Finally, they hypothesized that tetrasomic inheritance is likely to be important in the cultivated strawberry and should receive concurrent attention in interpreting the genetic data.

Powers (30) studied mieosis in hybrids between *Fragaria ovalis* and *F. ananassa* and observed autosyndesis, allosyndesis, or a combination of the two, and assumed that chromosome pairing in the octoploid species of *Fragaria* is probably genetically controlled. He also detected some asynaptic chromosomes and considered the importance of asynapsis and the conjugation

of more than two chromosomes to form multivalents during meiosis lies in the effect they have upon fruitfulness. By adversely affecting fruitfulness, asynapsis of the chromosomes during meiosis, if of frequent occurrence, may be one of the major factors contributing to the failure of a breeding program. Likewise, if homology exists between different genomes coming from the same polyploid species as well as between genomes coming from different polyploid species, conjugations of more than two chromosomes to form multivalents might be of frequent occurrence. If such were the case, one would expect fruitfulness to be reduced materially, possibly to the extent that the accomplishment of the objectives of the breeding programs would be threatened.

Rozanova (33) stated,

> ... it may be deduced that the evolution of species of *Fragaria* has proceeded in the direction of autopolyploidy or close allopolyploidy. From this, it follows that the hypothesis as to the origin of cultivated varieties from a cross between *F. virginiana* and *F. chiloensis* needs supplementing to the extent of stating that *F. virginiana* and *F. chiloensis* are also probably autoployploids or close allopolyploids with homologous genomes.

Scott (34) stated that tetraploid *Fragaria vesca* usually had some multivalents at metaphase I. Configurations frequently observed were quadrivalents, trivalents, and bivalents. Univalents, also, were observed in some cases. In hybrid hexaploids produced from a cross between *F. vesca* and cultivated strawberries, many meiotic irregularities were observed. Multivalents as well as univalents were frequent at metaphase I. Heptaploid selections were very irregular in meiosis.

Sebastiampillai and Jones (35) wrote:

> Cytogenetical studies in polyploids have been made by several workers with a view to assessing phylogenetic relationships. But interpretations and conclusions of these workers with regard to the nature of polyploids are not always in agreement.

In their studies, they found that the 28 chromosomes of the autotetraploids of *F. vesca* were associated as bivalents and quadrivalents at diakinesis and metaphase I. Trivalents or multivalents higher than quadrivalents were absent or rare. The mean frequency of quadrivalents per cell at metaphase I was consistently lower than that at diakinesis in each of the different tetraploids. Univalents were present in some cells. They also added, the interpretation of chromosome association at metaphase I was confused by the changes occurring in association as well as by the difficulty of analysis. The analysis of chromosome association at diakinesis is a more reliable indication of the maximum association, and subsequent comparisons were based as far as possible, on the frequencies of chromosome configuration observed at this stage.

Senanayake and Bringhurst (36) analyzed the hexaploids derived from crosses between the autotetraploid form of *Fragaria vesca* L. and the octoploid species, *F. chiloensis* and *F. virginiana*. They hypothesized that, if the octoploids have the diploid genome A, the hexaploid hybrids should have trivalents. Trivalents as well as quadrivalents were observed. They attributed the presence of quadrivalents to the possible pairing of the free chromosome arms of the 3A genomes with the chromosomes of the "C" genome. Furthermore, more than 14 bivalents in all hexaploid hybrids were present. They concluded, therefore, that the "C" genome of the octoploid *Fragaria*

probably is phylogenetically related to the A genome and modified the genomic formula for the octoploid strawberry species to AAA'A'BBBB.

Yamaguchi (38), from his work on six cultivars of strawberry in Japan, indicated that all cultivars had 56 chromosomes in somatic cells. He concluded that the chromosomes were so small (0.5μ to 1.5μ) that each set of homologous chromosomes could not be identified, and the cytological identification of each cultivar of strawberry is rather difficult. A camera lucida drawing of the somatic chromosomes of the cultivar Donner showed 7 satellite chromosomes. During the investigation of the somatic chromosomes of the seven-chromosome group of *Fragaria*, Yarnell (39) found some differences in the relative length of the chromosome pairs. It was difficult to estimate their length because of the small size, and their shape. He detected some association between the chromosomes as pairs, this association not only of chromosomes of equal or nearly equal length, but often of similar shape. The associations of homologies in the somatic tissue that he found were either end-to-end or parallel, and were evident in all of the species of this group.

The same author (40) studied meiosis in a triploid *Fragaria* ($2n = 21$). He found the chromosomes usually in groups of ten bivalents plus unpaired chromosome, instead of forming seven trivalents or seven bivalents plus seven univalents. At the second metaphase, in which both plates could be counted, 10 and 11 chromosomes were found most frequently. He concluded that there was complete pairing between nonhomologous chromosomes, a logical deduction from the counts at diakinesis and supported by the fact that chromosomes of different sizes were paired. Obviously, conditions

arise which promote the pairing of chromosomes that are not homologs. Also, he studied the meiosis of $F_1$ triploid obtained from a cross between a tetraploid and *F. collina* and found irregular behavior in prophase stages preceding diakinesis. In addition, consistent complete pairing of the chromosomes at metaphase was found. He assumed that the association of nonhomologs occurred when he hypothesized that if the 3 genomes of the triploid are represented as ABCDEFG, abcdefg, and $A_1B_1C_1D_1E_1F_1G_1$, two sets can pair as Aa, Bb, Cc, Dd, Ee, Ff, and Gg, or $AA_1$, $BB_1$, etc. Because of the complete pairing observed during meiosis, he expected another type of association to occur between the nonhomologous chromosomes of the unpaired third set as $A_1B_1$, $C_1D_1$, $E_1F_1$, and $G_1$ (41). However, the association between nonhomologous chromosomes in the triploids was not conducive to chromosomal exchange (43).

An unusual amount of chromosome pairing during the meiosis of the $F_1$ progenies from crosses between octoploid and diploid species of *Fragaria* was found by Yarnell (42). This pairing seemed to be partially correlated with temperature. In this matter he provided as evidence pairing not only between chromosomes from both parents, but also autosyndesis among the remaining sets of the octoploid parent. In addition, he found secondary association taking place between bivalents. He interpreted the formation of multivalents as a result of distinct homology of the chromosome sets from parental species.

# MATERIALS AND METHODS

The present work was carried out during the 1979 and 1980 growing seasons in the genetics and horticulture laboratories of the Iowa State University.

## Materials

Five seedlings each of four $F_1$ progenies of octoploid cultivated strawberries (*Fragaria* x *ananassa* Duch.) and their respective parental clones were selected for this study. The progenies were 7815 (6-75060 x 25-6943), 7836 (1-75004 x 25-6943), 7846 (21-6937 x 19-6935), and 7873 (19-6935 x 3-6969). The parents were 6-75060, 25-6943, 1-75004, 21-6937, 19-6935, and 3-6969.

## Methods

### Meiosis

Flower buds were collected in early stages of development from $F_1$ progenies and parental clones growing in the field during the spring of 1979 and 1980. Buds were fixed in propionic acid: absolute alcohol (1:2 v/v) and stored in a refrigerator (4°C). Buds were removed from the fixative, rinsed in distilled water, and anthers were macerated in a drop of 1% propionic-carmine stain, by placing a coverslip on the anthers and tapping the coverslip gently and carefully. If the diakinesis or metaphase I stages were observed, the slide was warmed very gently before being pressed vigorously between several layers of blotting paper. Squash preparations were temporarily preserved for examination by sealing the

edges of the coverslips with one of several wax base compounds. The prepared slides could be kept satisfactorily at room temperature for 10-15 days.

Slides were examined soon after preparation, and those with good figures were made permanent using the method of Bowen (4). This method uses liquid $CO_2$ applied directly on the bottom of the slide. While the preparation was still frozen, the coverslip was popped-off the slide with a sharp razor blade, and the slide simultaneously thawed and dehydrated by immersion in 95% ethanol for several minutes. With well-flattened preparations, free from large pieces of debris, little or no material adhered to the coverslip and it was set aside for cleaning and reclaiming. A drop of Euparal was placed on the drained slide and a clean, dry coverslip quickly lowered into position before the alcohol evaporated from the specimen.

Frequencies of the different chromosomal associations during diakinesis and metaphase I were determined and recorded for all the $F_1$ progenies and their parental clones. All data of this study were statistically analyzed using a $\chi^2$ test at 95% confidence level according to Snedecor and Cochran (37).

Mitosis

For determining the somatic chromosome numbers, roots 7 to 10 cm long were collected from the seedlings of all genotypes growing in the greenhouse. Only 1 cm of the root tip was excised and the last third of that tip was slit with a razor blade. Root tips were prefixed in a saturated aqueous solution of paradichlorobenzene (PDB) at 15°C for two hours. Then tips were washed with distilled water and placed in 95% ethanol:glacial

acetic acid (3:1 v/v) for 24 hours at room temperature. Tips were removed from the fixative and placed in 70% ethanol and stored in a refrigerator (4°C).

In preparation for staining, root-tips were removed from the 70% ethanol, washed with distilled water, then hydrolyzed for 15-20 minutes in 60°C 1 N hydrochloric acid. The acid was then removed and the roots were rinsed with distilled water and placed in Feulgen's stain in covered vials for 1-1½ hours. In order to intensify the staining of the chromosomes, the tips were placed in ice cold tap water for 20 minutes, and then transferred to pectinase (30°C) for 1 hour for softening the root tissue. Finally, the tip was placed on a slide and the unstained root cap was removed with a razor blade and discarded. Less than 1 mm of 1/2 of slit tip was placed in a drop of propio-carmine stain. The tip was tapped gently but thoroughly with glass rod, coverslip was applied and the slide was warmed and firmly pressed under filter paper. Slides were examined soon after preparation and slides with good figures were made permanent by the liquid carbon dioxide.

This procedure was developed for counting chromosomes in soybean by Palmer and Heer (29). The only modification necessary for counting strawberry chromosomes was increasing the duration of hydrolysis.

In all genotypes studied, counts were made in at least 10 slides. Somatic chromosome numbers were determined and recorded.

For counting the number of the nucleoli in mitotic interphase cells, the technique described by Rattenbury (31) was used. Root-tips were fixed for 24 hours in fluid consisting of 95% alcohol:formalin (2:1 v/v), and

glacial acetic acid to give a 5% concentration of total volume, and then stored in 70% alcohol until further use. The tips were washed with distilled water and placed in 1 N hydrochloric acid which was already at 60°C and were hydrolyzed at that temperature for 2 hours. The acid was removed and root-tips were washed a few times with distilled water. Less than 1 mm of the tip was placed in a drop of aceto-carmine stain; the tip was tapped gently with a glass rod, then a coverslip was applied, and the slide was warmed and firmly pressed under filter paper.

Best results were obtained by overstaining and destaining. The latter step was carried out by removing excess stain from the edges of the coverslip with a cloth moistened in 45% acetic acid, taking full care not to move the coverslip. Fresh 45% acetic acid was drawn under the cover glass with absorbent paper until the liquid surrounding the cells was colorless. Satisfactory preparations were made permanent using the technique described previously.

Photomicrographs were taken on a AO-Spencer Microstar Series 10 microscope with a 1053 A 35 mm camera. The Kodak high contrast copy film 5069 was developed in Kodak developer D-19 for 6 minutes at 20°C, fixed in Kodak fixer for 4 minutes, and washed in running water at 20°C for at least 30 minutes. Enlarged prints were made with a Beseler Model 45 M enlarger equipped with a Schneider Componon 50 mm lens.

## RESULTS

The frequencies of chromosomal associations in 1979 and 1980 in diakinesis are shown in Table 1 for the progenies and their parental clones. It is obvious that the chromosomes tended to pair as bivalents during this stage at a high frequency for all genotypes studied (Figure 1a). The frequencies of the PMCs with 28 bivalents ranged from 84.0% to 87.8% and from 89.9% to 92.3% for the progenies and the parental clones, respectively, in 1979, whereas the frequencies of the PMCs with 28 bivalents ranged from 84.8% to 87.6% and from 86.5% to 92.5% for the 4 $F_1$ progenies and their parents, respectively, in 1980.

During diakinesis, the configuration of the bivalents was either a rod or a ring. However, the ring configurations were the most common (Figure 1b). In certain PMCs, a few bivalents showed a loose association between the two chromosomes (Figures 1a, b, d). Five bivalents were associated with the nucleolus in a few PMCs (Figure 1b). However, most PMCs showed 3 or 4 bivalents associated wtih the nucleolus in all genotypes studied. Another deviation from the regular diakinesis was the presence of two nucleoli in a few PMCs (Figure 2b).

Univalents were detected in a few cases in both progenies and their parental clones (Figure 1c). The percentages of the PMCs with univalents during diakinesis in 1979 ranged from 0.0 to 6.2 and from 0.0 to 3.9 for $F_1$ progenies and their parents, respectively. In 1980, these percentages ranged from 0.6 to 4.3 for the progenies and from 0.6 to 3.8 for the parental clones.

Table 1. Chromosomal association during diakinesis for octoploid strawberry in 1979 and 1980

| Genotypes | | 1979 | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | No. of PMCs with | | | PMC observed (no.) | PMC with 28II (%) | Chromosomes in psm[z] | |
| Progenies | Parental clones | 28II | 27II + 2I | Psm[z] | | | (No.)[y] | (%) |
| 7815 | | 136 | 10 | 16 | 162 | 84.0 | 96 | 1.1 |
| | 6-75060 | 161 | 2 | 16 | 179 | 89.9 | 128 | 1.3 |
| | 25-6943 | 162 | 7 | 11 | 180 | 90.0 | 64 | 0.6 |
| 7836 | | 151 | 0 | 27 | 178 | 84.8 | 130 | 1.3 |
| | 1-75004 | 142 | 0 | 13 | 155 | 91.6 | 66 | 0.8 |
| | 25-6943 | 162 | 7 | 11 | 180 | 90.0 | 64 | 0.6 |
| 7846 | | 152 | 5 | 23 | 180 | 84.4 | 192 | 1.9 |
| | 21-6937 | 164 | 3 | 13 | 180 | 91.1 | 108 | 1.1 |
| | 19-6935 | 155 | 1 | 12 | 168 | 92.3 | 94 | 1.0 |
| 7873 | | 137 | 3 | 16 | 156 | 87.8 | 100 | 1.1 |
| | 19-6935 | 155 | 1 | 12 | 168 | 92.3 | 94 | 1.0 |
| | 3-6969 | 152 | 2 | 11 | 165 | 92.1 | 76 | 0.8 |

[z]Pseudomultivalents.

[y]Actual number of chromosomes involved in pseudomultivalents calculated from the original data.

| 1980 | | | | | | |
|---|---|---|---|---|---|---|
| No. of PMCs with | | | PMC observed (no.) | PMC with 28II (%) | Chromosomes in psm[z] | |
| 28II | 27II + 2I | Psm[z] | | | (No.)[y] | (%) |
| 137 | 7 | 16 | 160 | 85.6 | 74 | 0.8 |
| 129 | 3 | 16 | 148 | 87.2 | 106 | 1.3 |
| 135 | 6 | 15 | 156 | 86.5 | 86 | 1.0 |
| 128 | 1 | 22 | 151 | 84.8 | 138 | 1.6 |
| 157 | 1 | 8 | 166 | 94.6 | 42 | 0.5 |
| 135 | 6 | 15 | 156 | 86.5 | 86 | 1.0 |
| 126 | 2 | 12 | 140 | 90.0 | 82 | 1.0 |
| 170 | 2 | 11 | 183 | 92.9 | 88 | 0.9 |
| 144 | 3 | 11 | 158 | 92.3 | 66 | 0.7 |
| 149 | 1 | 20 | 170 | 87.6 | 124 | 1.3 |
| 144 | 3 | 11 | 158 | 92.3 | 66 | 0.7 |
| 160 | 1 | 12 | 173 | 92.5 | 66 | 0.7 |

Figure 1. Chromosomal associations of octoploid strawberry during diakinesis

a. PMC with 28 II. Arrows point to loose bivalents (x 2500)

b. PMC with 28 II. Big arrow points to a ring configuration and small arrow points to a loose bivalent. Note the five bivalents associated wtih the nucleolus (x 2400)

c. Secondary association between bivalents (big arrows). Note the 2 univalents (small arrows) (x 2550)

d. Secondary association between bivalents (big arrow); small arrow points to a loose bivalent (x 2600)

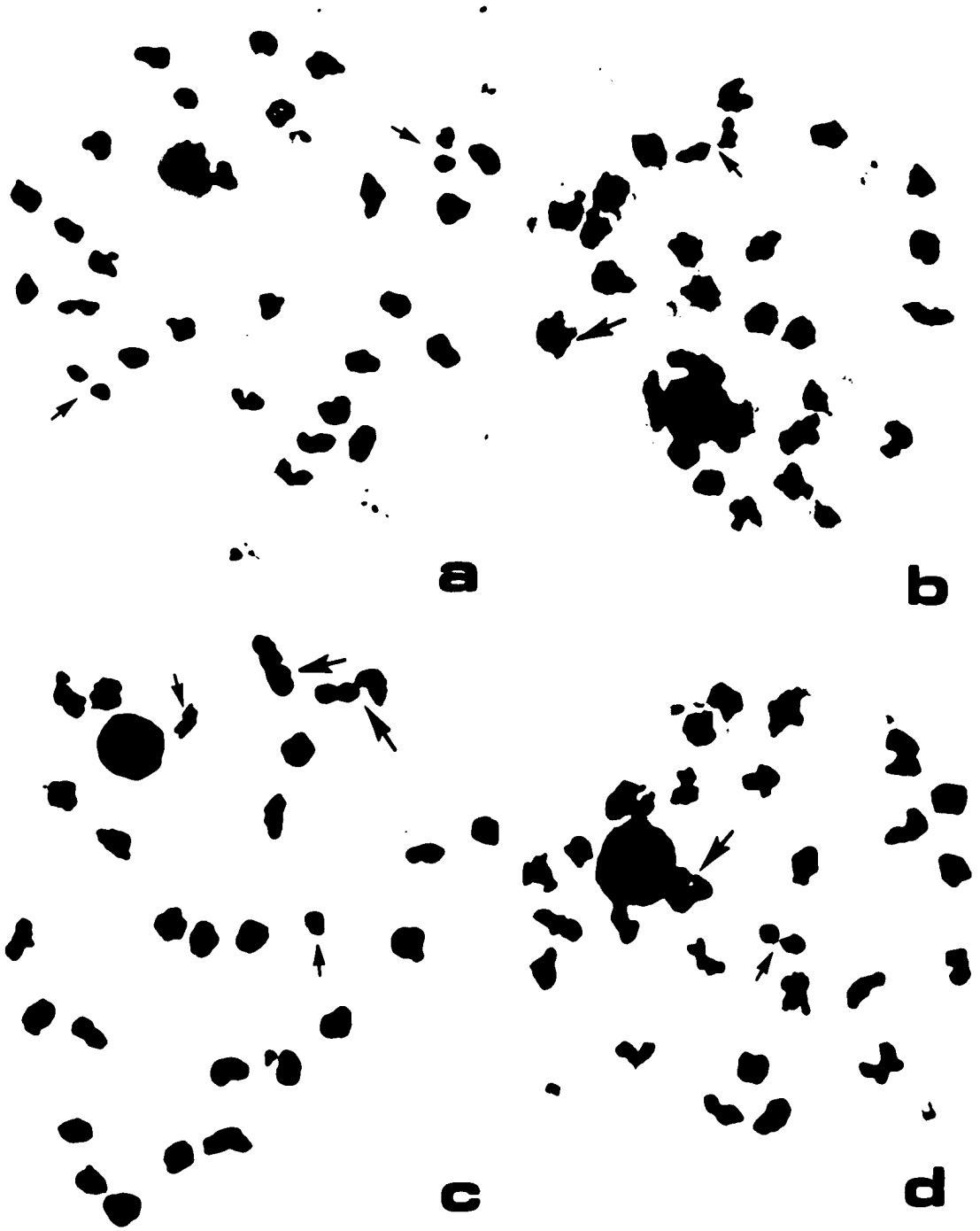

a
b
c
d

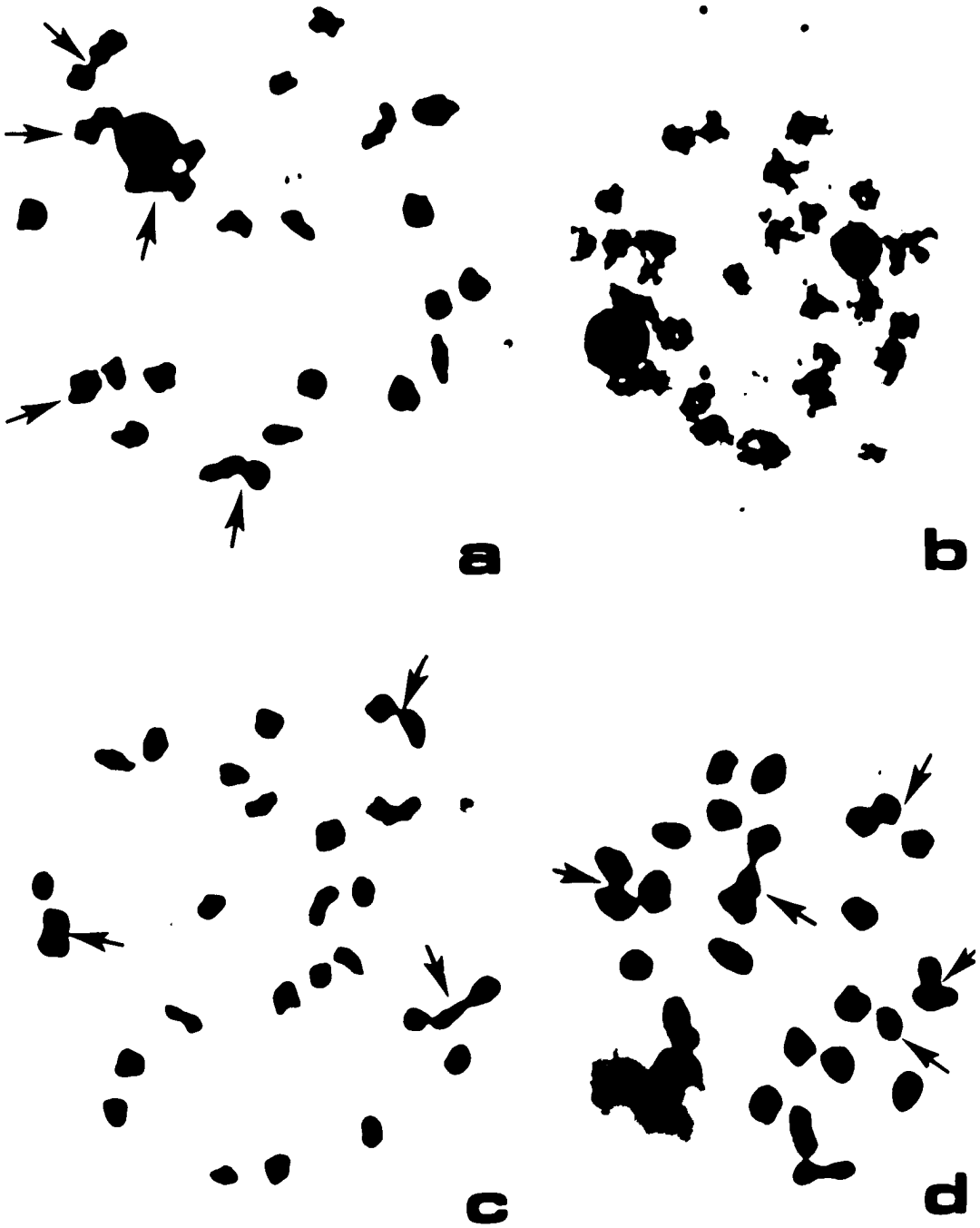
Figure 2. Chromosomal associations of octoploid strawberries during diakinesis and metaphase I

a. Secondary association between bivalents during diakinesis (arrow) - side-to-side association (x 2460)

b. Two nucleoli in the same PMC (x 2370)

c. Secondary association between bivalents during metaphase I (arrow) - side-to-side and end-to-end associations (x 2390)

d. Secondary association between bivalents during metaphase I (arrow) - end-to-side and side-to-side associations (x 3520)


a
b
c
d

The frequencies of chromosomal association in 1979 and 1980 in metaphase I were determined and recorded for all the genotypes studied. At this stage, the chromosomes were grouped on the metaphase plate. Twenty-eight bivalents were observed at metaphase I. The data presented in Table 2 show that chromosomal behavior during this stage for the four progenies and their parents was normal, and almost all the chromosomes paired as bivalents. The frequencies of the PMCs with 28 bivalents ranged from 90.6% to 95.8% for progenies and from 96.6% to 99.1% for parents in 1979. The frequencies in 1980 ranged from 91.8% to 94.5% and from 94.2% to 100.0% for the progenies and their parental clones, respectively. Univalents were not observed in metaphase I.

Secondary associations were scored in some PMCs. In all the genotypes studied, association between some bivalents were observed in some PMCs during diakinesis (Figure 1c, d; 2a) and metaphase I (Figure 2c, d). The data presented in Table 1 showed that during diakinesis, the percentages of PMCs with secondary association ranged from 9.9 to 15.2 and 6.1 to 8.9 in 1979 for the progenies and their parents, respectively. In 1980, these percentages were 8.9 to 14.6 for the $F_1$ progenies and 6.0 to 10.8 for the parental clones. Likewise, data in Table 2 indicate that secondary associations were observed during metaphase I in all genotypes studied. The frequencies of PMCs with secondary associations in 1979 ranged from 4.2% to 9.4% and from 0.9% to 3.4%; and in 1980 ranged from 5.5% to 8.2% and from 0.0% to 5.8% for the progenies and parental clones, respectively.

In these configurations, the types of the association were end-to-end, end-to-side, or side-to-side, but not ring or chain of four

Table 2. Chromosomal association during metaphase I for octoploid strawberry in 1979 and 1980

| Genotypes | | 1979 | | | | | |
|---|---|---|---|---|---|---|---|
| | | No. of PMCs with | | PMC observed | PMC with 28II | Chromosomes in psm[z] | |
| Progenies | Parental clones | 28II | Psm[z] | (no.) | (%) | (no.)[y] | (%) |
| 7815 | | 120 | 7 | 127 | 94.5 | 48 | 0.7 |
| | 6-75060 | 111 | 1 | 112 | 99.1 | 4 | 0.1 |
| | 25-6943 | 86 | 3 | 89 | 96.6 | 28 | 0.6 |
| 7836 | | 158 | 7 | 165 | 95.8 | 48 | 0.5 |
| | 1-75004 | 119 | 3 | 122 | 97.5 | 14 | 0.2 |
| | 25-6943 | 86 | 3 | 89 | 96.6 | 28 | 0.6 |
| 7846 | | 97 | 6 | 103 | 94.2 | 50 | 0.9 |
| | 21-6937 | 102 | 3 | 105 | 97.1 | 26 | 0.4 |
| | 19-6935 | 116 | 2 | 118 | 98.3 | 12 | 0.2 |
| 7873 | | 115 | 12 | 127 | 90.6 | 96 | 1.3 |
| | 19-6935 | 116 | 2 | 118 | 98.3 | 12 | 0.2 |
| | 3-6969 | 105 | 3 | 108 | 97.2 | 12 | 0.2 |

[z]Pseudomultivalents.

[y]Actual number of chromosomes involved in pseudomultivalents calculated from the original data.

| 1980 | | | | | |
|---|---|---|---|---|---|
| No. of PMCs with | | PMC observed | PMC with 28II | Chromosomes in psm[z] | |
| 28II | Psm[z] | (no.) | (%) | (No.)[y] | (%) |
| 146 | 12 | 158 | 92.4 | 92 | 1.0 |
| 97 | 2 | 99 | 98.0 | 12 | 0.2 |
| 105 | 1 | 106 | 99.1 | 4 | 0.1 |
| 156 | 9 | 165 | 94.5 | 66 | 0.7 |
| 116 | 2 | 118 | 98.3 | 14 | 0.2 |
| 105 | 1 | 106 | 99.1 | 4 | 0.1 |
| 112 | 8 | 120 | 93.3 | 54 | 0.8 |
| 97 | 6 | 103 | 94.2 | 42 | 0.7 |
| 128 | 0 | 128 | 100.0 | 0 | 0.0 |
| 89 | 8 | 97 | 91.8 | 72 | 1.3 |
| 128 | 0 | 128 | 100.0 | 0 | 0.0 |
| 95 | 4 | 99 | 96.0 | 26 | 0.5 |

configurations as expected (Figure 2a, c and d). Moreover, the physical appearance of these apparent associations indicated that they probably were formed as a result of aggregation of two or three bivalents. Hence, these configurations were pseudomultivalents, not true multivalents. Although the percentages of PMCs with pseudomultivalents were relatively greater for both progenies and their parental clones during diakinesis and metaphase I, the actual numbers of chromosomes involved in pseudomultivalent formation were low, relative to the total number of chromosomes in PMCs examined. In diakinesis, the percentages of chromosomes involved in pseudomultivalents in 1979 ranged from 1.1 to 1.9 for progenies and from 0.6 to 1.3 for parents; in 1980, the percentages ranged from 0.8 to 1.6 and from 0.5 to 1.3 for progenies and parental clones, respectively. In metaphase I, these percentages were slightly different. In 1979, the percentages ranged from 0.5 to 1.3 and from 0.1 to 0.6 for progenies and parents, respectively. The percentages for the progenies ranged from 0.7 to 1.3 and for the parents from 0.0 to 0.7 in 1980.

The chromosome associations observed in this study indicated that meiosis was completely normal for the 4 progenies and their parents. The stages preceding diakinesis were normal, in leptotene chromosomes were long and slender, and in pachytene, the chromosomes were distinctly thicker. In diplotene stage, the chromosomes were much thicker and shorter than in previous stages. Also, the stages after metaphase I were normal and the behavior of the chromosomes was regular. At the first anaphase, 28 chromosomes moved to each pole. Generally, all genotypes studied showed normal anaphase I except for a lagging chromosome in one anaphase I cell in

progeny 7846. At the beginning of telophase I, the chromosomes at each pole were accompanied by the formation of the cell wall. Then the second division started and the end result of this division was the production of four spores each containing 28 chromosomes, and surrounded by a cell wall. The wall of the mother cell, however, soon disintegrated leaving the microspores free in the cavity of the anther. Chi-square test at 95% confidence level showed no significant differences in the frequency of PMCs with 28 bivalents between 1979 and 1980 for both diakinesis and metaphase I. In this matter, also, there were no significant differences between the progenies and their parental clones.

Root-tip squashes of the four progenies and the parental clones revealed that mitosis was normal for all genotypes. All had 56 somatic chromosomes (Figure 3a, b). However, a few cells of progeny 7873 and its parent 3-6969 had double the chromosome number (Figure 3c, d). The chromosomes were about 0.5 μ to 1.5 μ long. Their relative length as well as differences in their size were not always clearly apparent. Two satellite chromosomes were detected for all the genotypes studied (Figure 3e). The findings of the present study indicated that all $F_1$s and their respective parents are octoploid with $2n = 8x = 56$ chromosomes.

With regard to the number of nucleoli per nucleus, the observations obtained using the aceto-carmine technique indicated that the number of nucleoli in interphase nucleus ranged from 1-8 for all progenies and their parental clones (Figure 3f).

Figure 3. Mitosis of octoploid strawberries

a-b. Somatic cells with 56 chromosomes (Note: A few metacentric and subtelocentric chromosomes can be seen in Figure a)

c. Somatic cell with double the 2n chromosome number in the progeny 7873

d. Somatic cell with double the 2n chromosome number in the parent 3-6969

e. Somatic cell with 56 chromosomes. Note the two satellite chromosomes (arrows)

f. Interphase nucleus with many nucleoli -- all bars denote 10 μ


a
b
c
d
e
f

# DISCUSSION

The results obtained in this study clearly show that the chromosomes were exclusively associated as bivalents during diakinesis and metaphase I and confirm the work of Byrne and Jelenkovic (5), Ichijima (15) and Powers (30). However, these findings are not in agreement with the work of Mok and Evans (26) who indicated that most of the chromosomes were associated as multivalents in 54%-71% of the PMCs observed. The discrepancy between the results of different investigators might be due to different methods of handling and examining the PMCs. Therefore, the formation of apparent multivalents might be due to difficulties in technique, such as poor fixation or inadequately flattened PMCs, which would make it difficult to distinguish between true multivalents and pseudomultivalents (5).

Regular bivalent formation during meiosis indicated that the chromosomes of cultivated octoploid strawberry have undergone cytological diploidization. This conclusion is in complete agreement with the work of Byrne and Jelenkovic (5), who stated that genetic corollary of such a pairing pattern in the octoploid *F.* x *ananassa* is that the genes will segregate according to independent chromosome assortment and not according to chromatid assortment as would be expected if there were regular multivalent formation. Also, the work of Richardson (32) on the progenies of *F. chinensis* x *F. chiloensis* indicated that the segregation of normal to variegated foliage fit a 3:1 ratio. However, tetrasomic inheritance is also likely to be important in the cultivated strawberry and should be considered in the interpretation of genetic data (26).

According to the configurations observed in the present study, the type of association, as well as the failure to detect chiasmata formation, indicated that pseudomultivalents were probably formed by mere physical proximity. If these configurations were the result of genuine synapsis and chiasmata formation, one would expect to find quadrivalents, trivalents + univalents or hexavalents. Such configurations require a minimum number of chiasmata for formation of the multivalents. Configurations such as heptavalents and octavalents would require a much higher number of chiasmata, and due to the small chromosome size, are less likely to be formed. Therefore, the physical appearance of these configurations observed in this study showed that they were merely aggregation of regular bivalents. Hence, these configurations are not true multivalents, but pseudo-multivalents. This conclusion is supported by the work of Byrne and Jelenkovic (5). The recent work of Jelenkovic et al. (16) in *Ricinus communis* indicated that nucleolar-like material contributed to the clumping tendency among nonhomologous univalents. In *Zea mays*, Majumder and Sarkar (25) attributed the pseudo-association resulting from stickiness of chromosomes as possibly due to heterochromatin. This kind of secondary association between bivalents during meiosis has been observed in *Aegilops triaristata* (22).

There seems to be no definite evidence that these configurations reflect the degree of homology between the genomes of cultivated octoploid strawberries. The question is whether the absence of multivalents is due to the lack of homoeology between the chromosomes or to other factors controlling the bivalent pairing pattern. Although the three basic chromosome

sets of the hexaploid *F. moschata* are homologous, multivalents were not observed during diakinesis (2). The chromosome associations in the pentaploid hybrid between *F.* x *ananassa* x *F. nubicola* indicated that some of the chromosomes contributed by *F.* x *ananassa* displayed homoeology (5). Whether the pseudo-multivalents observed in the present study are or are not related to homoeology was not resolved. However, the work of Kempanna and Riley (20) indicated that secondary association in *Triticum aestivum* is dependent upon the genetic relationship of the associated bivalents.

Although homoeology exists among the genomes of the octoploid *F. ananassa* (5, 36), the reason for the absence of multivalents is not clear. The most satisfactory explanation was offered by Byrne and Jelenkovic (5) based upon preferential pairing, i.e., only homologous chromosomes pair (A with A, A' with A', B with B), whereas, homoeologous chromosomes never pair (A with A', A with B, A' with B). If such a controlling system were operating, at least occasional multivalents would be expected for chromosomes of the B genome present in two sets. Therefore, one must be cautious in interpreting the various chromosome configurations observed since the pairing behavior is often influenced by several environmental and genetic factors apart from true homology (19). Also, the effect of the environmental factors on the chromosomal association has been detected by other workers (3, 18, 21, 41).

The results of this study indicated that the second division stages of meiosis are completely normal and, in this regard, agree with the findings of Mok and Evans (26), who concluded that the meiotic cycle following diakinesis in *F.* x *ananassa* is normal.

It is not clear whether the presence of different number of bivalents associated with the nucleolus during diakinesis is due to poor techniques in flattening PMCs or to other causes. However, the results of this study agree with those observed by Byrne and Jelenkovic (5), who found that the number of bivalents associated with the nucleolus during diakinesis ranged from 1 to 7 bivalents. Cytological studies of mitosis, especially of the number of secondary constriction of the strawberry satellited chromosomes which represent the nucleolus organizing region, may be helpful in answering this question.

Mitosis in root tip cells indicated that all the genotypes studied possess the somatic chromosome number, $2n = 56$. In this matter, these observations agree wtih the results of Yamaguchi (38), who found that all six octoploid cultivars he studied had 56 chromosomes in somatic cells. Generally speaking, all the stages of the mitosis were normal for all the progenies and their parental clones. The only deviation from the normal mitosis was the detection of some somatic cells in the progeny 7873 and the parent 3-6969 with double the $2n = 56$ chromosome number. The possible explanation for this case is the failure of the formation of new cell wall to separate the two daughter cells (endomitosis). Two satellite chromosomes were observed in this study for all the genotypes studied. However, in one camera lucida drawing of the cultivar Donner, 7 satellite chromosomes were illustrated by Yamaguchi (38). The very small chromosomes and little difference in their relative length, make it impossible or very difficult to identify each set of homologous chromosomes with the techniques presently available. Also, the results of the present study indicated that there was no cytological difference among the genotypes studied.

The number of nucleoli per nucleus was different from cell to cell; it ranged from 1 to 8 for all the 4 progenies and their respective parental clones. Nicoloff et al. (28) reported that the primary nucleoli in the nucleus apparently follow a definite pattern of fusion which seems to be coupled with the progression of the cells through the cell cycle.

# SUMMARY AND CONCLUSIONS

The present study was carried out on four octoploid cultivated strawberry progenies and their parental clones (*Fragaria* x *ananassa* Duch.) during the seasons of 1979 and 1980. The results obtained indicated that chromosomal behavior during meiosis as well as during mitosis was normal for all the $F_1$ progenies and their parents. For all genotypes studied, the chromosomes were associated as bivalents during the stages of diakinesis and metaphase I at high frequency. Secondary associations between bivalents were observed in both stages for all the progenies and their respective parents. However, the configurations of these associations were only end-to-end, end-to-side, or side-to-side, but not ring or chain configurations. The physical appearance of these configurations, therefore, indicated that they are probably formed by the aggregation of bivalents. Hence, these configurations are pseudomultivalents, not genuine multivalents.

Whether these secondary associations are related to homoeology among the four genomes of *F. ananassa* is not known. The observations obtained during this study indicated that there is no definite evidence that these configurations reflect the relationship between the genomes of the cultivated octoploid strawberries.

Loose bivalents and(or) univalents were observed in some pollen mother cells (PMCs) during diakinesis. Also, during this stage, two nucleoli were observed in a few PMCs. Different numbers of bivalents associated with the nucleolus of the diakinesis were observed. These numbers were different from one PMC to another; however, five bivalents was the common

number that associated with the nucleolus for all the progenies and their parents.

Twenty-eight bivalents in diakinesis indicated that the progenies and their parents are octoploid, with $2n = 8x = 56$ chromosomes.

The cytological observations obtained during this study showed that all the stages of meiosis that precede diakinesis, also all the stages after metaphase I, including the second meiotic division, were completely normal for all the genotypes studied. The only exception from this generalization was a lagging chromosome in one anaphase I cell in the progeny 7846.

The study of the chromosomal behavior during mitosis indicated that all the four progenies and their parental clones possess somatic chromosome number equal to 56. However, some somatic cells containing the double chromosome number detected in the progeny 7873 and its parent 3-6969. Generally, all the stages of mitosis were normal for all the genotypes studied.

The possible number of satellite chromosomes detected during this work was only two for all the $F_1$ progenies and their respective parental clones.

Last, but not least, the number of nucleoli per nucleus differs from cell to cell; it ranged from 1 to 8 for all the four progenies and their parents. It seems that the number of nucleoli per nucleus decreases with the progression of the cell cycle.

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# CONCLUSIONS

Since the vegetative propagation considered the most common method for strawberry production, mating of the phenotypically selected parental clones followed by selection among their superior offspring may be the most expedient method for breeding strawberries for adaptability to machine harvest. In evaluating eighteen progenies and their parents for yield, concentration of fruit ripening, berry firmness, and easy-cap characters, it was found that matings between the selected phenotypes affected these traits.

In certain progenies, mating of selected clones increased significantly the average number of berries per plant as compared to the mean averages for both parents. However, some other progenies showed no differences, or lower averages than those obtained by their own parents. For the most genotypes studied, the average number of berries, as well as the percentage of ripe berries, changed throughout the four harvests. The percentages of ripe berries, however, reached a peak during the second and third harvests. The relationship between yield and concentrated ripening traits was strong that the high yielding genotypes concentrated high percentages of their berry ripening within a short period of time. It was found that, if the two parental clones were highly concentrated ripening, usually their progeny was highly concentrated, contrasted with one high and one low concentrated ripening paretns.

The average berry firmenss was affected by the crosses between the parental clones; it was found in many cases the average berry firmness for the progeny exceeded the mean averages of both parents. These progenies

are considered as candidates for mechanical harvest. Moreover, some other matings decreased berry firmness, or showed no differences between the progeny and its parental clones. Also, easy-cap trait (the average force required for berry detachment) was affected by the parental matings. The results of the present study indicated that some progenies had higher averages of force required for berry detachment than the mean averages of their own parental clones and, consequently, these progenies are considered as noneasy-cap, whereas some other progenies had averages of force required for berry detachment less than that obtained by their parental clones, and they are considered easy-cap types.

The average of berry firmness and the capping force were decreased significantly from one harvest date to the next for most of the genotypes studied. A strong relationship was detected between berry firmness and easy-cap traits. It was found the easy-cap types which required less force for berry detachment usually had soft berries. The genes which control these characters seem to be linked together.

The results obtained from the cytogenetical study indicated that chromosomal behavior during meoisis as well as during mitosis was normal for the four progenies and their respective parents. For all genotypes studied, chromosomes were exclusively associated as bivalents at diakinesis and metaphase I. Secondary associations between bivalents were observed in both stages for all genotypes. However, the configurations of these associations were only end-to-end, end-to-side, or side-to-side, but not ring or chain configurations. The physical appearance of these configurations, therefore, indicated that they are probably formed by the aggregation of bivalents. Hence, these configurations are pseudomultivalents,

not true multivalents. Whether these secondary associations are related to homoeology among the four genomes of *F. ananassa* is not known.

Loose bivalents and (or) univalents were observed in some pollen mother cells (PMCs) during diakinesis. Also, during this stage, two nucleoli were observed in a few PMCs. Different numbers of bivalents associated with the nucleolus of the diakinesis were observed. These numbers were different from one PMC to another; however, five bivalents was the common number that associated with the nucleolus for all the progenies and their parents. Twenty-eight bivalents in diakinesis indicated that the progenies and their parents are octoploid, with 2n=8x=56 chromosomes. All stages of meiosis that precede diakinesis, also all the stages after metaphase I, including the second meiotic division were normal.

The study of mitosis indicated that all the four progenies and their parents possess somatic chromosome number equal to 56. However, some somatic cells containing the double chromosome number detected in the progeny 7873 and its parent 3-6969. Generally, all the stages of mitosis were normal for all the genotypes studied. The number of satellite chromosomes detected during this work was only two for all genotypes studied. The number of nucleoli per nucleus differs from cell to cell; it ranged from 1 to 8. It seems that the number of nucleoli per nucleus decreases with the progression of the cell cycle.

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# APPENDIX

Figure A-1. Chatillon Fruit and Vegetable Tester with a 1000 g capacity, in 10 g units was used for measuring capping force (a, b), and for measuring berry firmness (c, d)

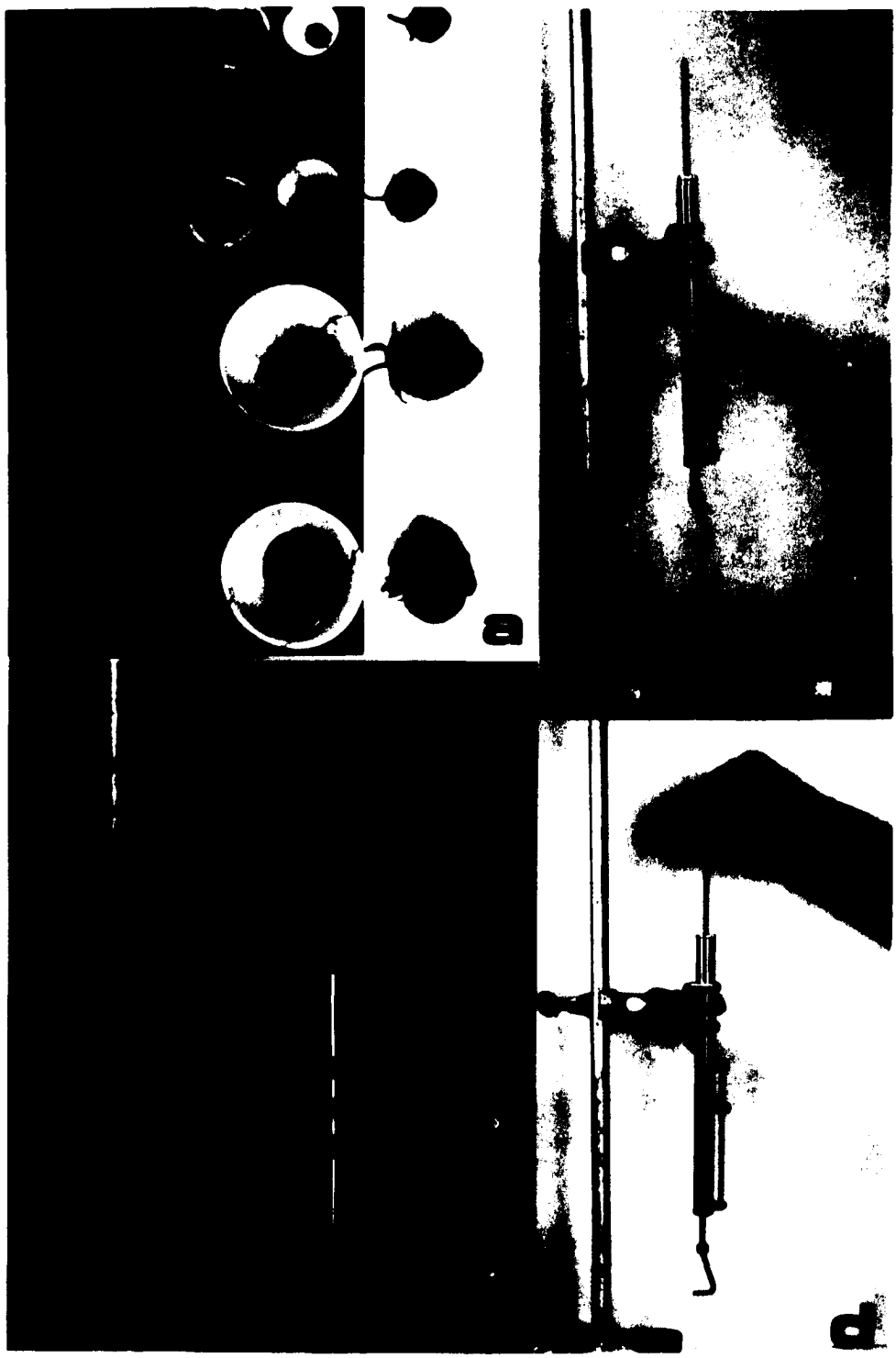
a
d

Table A-1. Analyses of variance for yield (average number of berries per plant) in 1980

| Source | d.f. | S.S. | M.S. | "F" |
|---|---|---|---|---|
| Progenies vs. parents comparison | | | | |
| Replications | 1 | 0.62 | | |
| Entities | 43 | 7242.00 | 168.4 | 104.0** |
| Among progenies | (17) | 3335.00 | 196.2 | 121.1** |
| Among parents | (25) | 3355.00 | 134.2 | 82.8** |
| Progenies vs. parents | ( 1) | 552.00 | 552.0 | 340.0** |
| Error | 43 | 70.00 | 1.63 | |
| Progenies vs. own parents comparison | | | | |
| Replications | 1 | 0.62 | | |
| Entities | 43 | 7242.00 | 168.40 | |
| Progenies vs. own parents | ( 1) | 636.00 | 636.00 | 390.2** |
| Remainder | (42) | 6606.00 | | |
| Error | 43 | 70.00 | 1.63 | |

**Significant at P = .001.

Table A-2. Analyses of variance for yield (average number of berries per plant) in 1981

| Source | d.f. | S.S. | M.S. | "F" |
|---|---|---|---|---|
| Progenies vs. parents comparison | | | | |
| Replications | 1 | 0.46 | | |
| Entities | 43 | 7168.16 | 166.70 | 166.70** |
| Among progenies | (17) | 3368.00 | 198.12 | 198.12** |
| Among parents | (25) | 3283.00 | 131.32 | 131.32** |
| Progenies vs. parents | ( 1) | 517.00 | 517.00 | 517.00** |
| Error | 43 | 43.07 | 1.00 | |
| Progenies vs. own parents comparison | | | | |
| Replications | 1 | 0.46 | 0.46 | |
| Entities | 43 | 7168.16 | 166.70 | |
| Progenies vs. own parents | ( 1) | 593.00 | 593.00 | 593.00** |
| Remainder | (42) | 6575.00 | | |
| Error | 43 | 43.1 | 1.00 | |

**Significant at P = .001.

Table A-3. Analyses of variance for firmness means in 1980

| Source | d.f. | S.S. | M.S. | "F" |
|---|---|---|---|---|
| **Progenies vs. parents comparison** | | | | |
| Replications | 1 | 600 | | |
| Entities | 43 | 969482 | 22546 | 127.9** |
| Among progenies | (17) | 748182 | 44010 | 249.6** |
| Among parents | (25) | 201792 | 8072 | 45.8** |
| Progenies vs. parents | ( 1) | 19508 | 19508 | 110.7** |
| Error | 43 | 7580 | 176.3 | |
| **Progenies vs. own parents comparison** | | | | |
| Replications | 1 | 600 | | |
| Entities | 43 | 969482 | 22546.0 | |
| Progenies vs. own parents | ( 1) | 25889 | 25889.0 | 148.8** |
| Remainder | (42) | 943593 | | |
| Error | 43 | 7580 | 176.3 | |

**Significant at P = .001.

Table A-4. Analyses of variance for firmness means in 1981

| Source | d.f. | S.S. | M.S. | "F" |
|---|---|---|---|---|
| **Progenies vs. parents comparison** | | | | |
| Replications | 1 | 696 | | |
| Entities | 43 | 958467 | 22290 | 106.7** |
| Among progenies | (17) | 734660 | 43215 | 206.8** |
| Among parents | (25) | 203102 | 8124 | 38.9** |
| Progenies vs. parents | ( 1) | 20705 | 20705 | 99.1** |
| Error | 43 | 8997 | 209 | |
| **Progenies vs. own parents comparison** | | | | |
| Replications | 1 | 696 | | |
| Entities | 43 | 958467 | 22290 | |
| Progenies vs. own parents | ( 1) | 27624 | 27624 | 132.2** |
| Remainder | (42) | 930843 | | |
| Error | 43 | 8997 | 209 | |

**Significant at P = .001.

Table A-5. Analyses of variance for capping force means in 1980

| Source | d.f. | S.S. | M.S. | "F" |
|---|---|---|---|---|
| Progenies vs. parents comparison | | | | |
| Replications | 1 | 350 | | |
| Entities | 43 | 812066 | 18885 ← | 50.3** |
| Among progenies | (17) | 639277 | 37605 ← | 100.1** |
| Among parents | (25) | 165792 | 6632 ← | 17.7** |
| Progenies vs. parents | ( 1) | 6997 | 6997 ← | 18.6** |
| Error | 43 | 16145 | 375.5 | |
| Progenies vs. own parents comparison | | | | |
| Replications | 1 | 350 | | |
| Entities | 43 | 812066 | 18885 | |
| Progenies vs. own parents | ( 1) | 17502 | 17502 ← | 46.61** |
| Remainder | (42) | 794564 | | |
| Error | 43 | 16145 | 375.5 | |

**Significant at P = .001.

Table A-6. Analyses of variance for capping force means in 1981

| Source | d.f. | S.S. | M.S. | "F" |
|---|---|---|---|---|
| **Progenies vs. parents comparison** | | | | |
| Replications | 1 | 494 | | |
| Entities | 43 | 305255 | 18727 ← | 40.76** |
| Among progenies | (17) | 627232 | 36896 ← | 80.30** |
| Among parents | (25) | 167914 | 6217 ← | 14.62** |
| Progenies vs. parents | ( 1) | 10109 | 10109 ← | 22.00** |
| Error | 43 | 19756 | 459.44 ← | |
| **Progenies vs. own parents comparison** | | | | |
| Replications | 1 | 494 | | |
| Entities | 43 | 805255 | 18727 | |
| Progenies vs. own parents | ( 1) | 21968 | 21968 ← | 47.81** |
| Remainder | (42) | 783287 | | |
| Error | 43 | 19756 | 459.44 ← | |

**Significant at P = .001.

Table A-7. Split plot analyses of variance of yield (average number of berries per plant) and harvest in 1980 and 1981

| Source | d.f. | S.S. | M.S. | "F" |
|---|---|---|---|---|
| | | 1980 | | |
| Replications | 1 | 0.16 | | |
| Entities | 43 | 1811.00 | 42.11 | 104.17** |
| Rep * Entities (Ea) | 43 | 17.38 | 0.4042 | |
| Harvest | 3 | 8410.61 | 2803.50 | 8021.50** |
| LIN | (1) | 6.77 | 6.77 | |
| Quad | (1) | 8365.50 | 8365.50 | |
| LOF | (1) | 40.13 | 40.13 | |
| Entity * Harvest | 129 | 2486.00 | 19.20 | 55.14** |
| Rep * Harvest (Eb) | 3 | 0.74 | 0.3495 | |
| Rep * Entity * Harvest (Eb) | 129 | 45.39 | | |
| | | 1981 | | |
| Replications | 1 | 0.11 | | |
| Entities | 43 | 1792.00 | 41.67 | 166.36** |
| Rep * Entity (Ea) | 43 | 10.77 | 0.2504 | |
| Harvest | 3 | 8220.17 | 2740.10 | 5436.62** |
| LIN | (1) | 15.5 | 15.5 | |
| Quad | (1) | 8147.0 | 8147.0 | |
| LOF | (1) | 50.3 | 50.3 | |
| Entity * Harvest | 129 | 2506.94 | 19.4 | 38.56** |
| Rep * Harvest (Eb) | 3 | 1.41 | 0.504 | |
| Rep * Entity * Harvest (Eb) | 129 | 65.11 | | |

**Significant at P = .001.

Table A-8. Split plot analyses of variance of average berry firmness and harvest in 1980 and 1981

| Source | | d.f. | S.S. | M.S. | "F" |
|---|---|---|---|---|---|
| | | 1980 | | | |
| Replications | | 1 | 2399 | | |
| Entities | | 43 | 3877927 | 90184 | 127.89** |
| Rep * Entity (Ea) | | 43 | 30322 | 705.2 | |
| Harvest | | 3 | 130665 | 43555 | 1514.9 ** |
| LIN | | (1) | 130557 | 130557 | 4541.1 ** |
| LOF | | (2) | 108 | 54 | 1.9 |
| Entity * Harvest | | 129 | 11499 | 89.14 | 3.10** |
| Rep * Harvest | (Eb) | 3 | 231 | 28.75 | |
| Rep * Entity * Harvest | (Eb) | 129 | 3564 | | |
| | | 1981 | | | |
| Replications | | 1 | 2782 | | |
| Entities | | 43 | 3833869 | 89159.7 | 106.53** |
| Rep * Entity (Ea) | | 43 | 35988 | 836.93 | |
| Harvest | | 3 | 132550 | 44183.33 | 1803.4 ** |
| LIN | | (1) | 132297 | 132297 | 5399.9 ** |
| LOF | | (2) | 253 | | 5.1 |
| Entity * Harvest | | 129 | 8729 | | 2.76** |
| Rep * Harvest | (Eb) | 3 | 205 | 24.5 | |
| Rep * Entity * Harvest | (Eb) | 129 | 3029 | | |

**Significant at P = .001.

Table A-9. Split plot analyses of variance of the average capping force and harvest in 1980 and 1981

| Source | | d.f. | S.S. | M.S. | "F" |
|---|---|---|---|---|---|
| | | 1980 | | | |
| Replications | | 1 | 803 | | |
| Entities | | 43 | 3288643 | 76480 | 50.71** |
| Rep * Entity (Ea) | | 43 | 64861 | 1508 | |
| Harvest | | 3 | 217936 | 72645 | 1315.00** |
| LIN | | (1) | 217828 | 217828 | 3943.3 ** |
| LOF | | (2) | 108 | | 0.98 |
| Entity * Harvest | | 129 | 22351 | 173.3 | 3.14** |
| Rep * Harvest | (Eb) | 3 | 213 | 55.24 | |
| Rep * Entity * Harvest | (Eb) | 129 | 7079 | | |
| | | 1981 | | | |
| Replications | | 1 | 1977 | | |
| Entities | | 43 | 3221021 | 74907.47 | 40.75** |
| Rep * Entity (Ea) | | 43 | 79024 | 1838 | |
| Harvest | | 3 | 230334 | 5356.60 | 1566.00** |
| LIN | | (1) | 230136 | 230136 | 4691.8 ** |
| LOF | | (2) | 198 | | 2.01 |
| Entity * Harvest | | 129 | 21562 | | 3.41 |
| Rep * Harvest | (Eb) | 3 | 219 | 49.04 | |
| Rep * Entity * Harvest | (Eb) | 129 | 6254 | | |

**Significant at P = .001.